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Created in 1849, the U.S. Department of the Interior is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

As the Nation's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States—now and in the future.

LIFE HISTORY OF LAKE HERRING IN LAKE SUPERIOR

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ABSTRACT

The average annual commercial catch of lake herring (*Coregonus artedi*) in U.S. waters of Lake Superior was nearly 12 million pounds in 1929–61. This production contributed 62.4 percent of the total U.S. take of lake herring for the Great Lakes. About 90 percent of the annual catch is taken from small-mesh gill nets during the November-December spawning season.

The life-history studies were based on 12,187 fish collected in 1950–62; past growth was computed for 3,779 specimens collected from commercial landings at: Duluth, Minn.; Bayfield, Wis.; and Portage Entry and Marquette, Mich.

Age group IV dominated the catch in each year's collection at each port, followed by age groups III and V. The average age of the lake herring in the commercial samples was 3.9 years at Bayfield, Portage Entry, and Marquette, and 4.1 years at Duluth. With few exceptions, the mean age of the females exceeded that of the males.

The strength of the year classes varied considerably at each port but generally declined over the 1946–55 period. Fluctuations were similar at Bayfield and Marquette, but at neither port resembled closely the fluctuations at Portage Entry. Year classes 1954 and 1955 were, however, well below average at all three ports.

Females were larger than males (largest difference was 0.6 inch) at all ports except Marquette where the males held a slight advantage. With only one exception, the average lengths of the age groups were larger in 1956–59 than in 1950–55. The largest increase from the earlier to the later period was 1.1 inches for the V-group males at Portage Entry. In general, the average size of the lake herring increased from the western to the eastern part of the lake.

The weight of the lake herring in the combined samples increased as the 3.170 power of the length. Lake herring of corresponding lengths were heavier in 1956–61 than in 1950–55 (greatest increase was 8.8 percent at Bayfield). Port-to-port differences in average weight among fish of the same length in 1950–55 showed a west-to-east trend toward increased weight.

The calculated lengths and weights of fish from Duluth were smallest, followed by those from Bayfield, Portage Entry, and Marquette. With only one exception, the calculated lengths and weights of lake herring taken in 1956–59 were greater than those taken in 1950–55.

The trends in annual fluctuations of growth in length and weight were closely correlated among the three ports. Growth was generally below average in 1945–53 and above average in 1954–59.

The percentage of females equalled or exceeded that of the males in all age groups above I. The percentage of females, all age groups combined, was 68.5. The first mature males appeared in the 8.5- to 8.9-inch group; the first mature females were in the 9.5- to 9.9-inch group. All males were mature at lengths greater than 11.4 inches, and all females at lengths greater than 11.9 inches. The youngest mature lake herring belonged to age group II, and all fish older than age group III were mature. Spawning of Lake Superior lake herring normally is at its peak during the last week in November and the first week in December. The average number of eggs produced by female Lake Superior lake herring was 6,351.

Crustacea were the most common food and were found in 83 percent of the 146 stomachs examined.

The distribution of lake herring may be influenced by temperature, abundance of plankton, and spawning. The fish are most common near the surface in early summer, migrate to deeper water as the surface water warms, and are randomly distributed between the surface and about 20 fathoms in the late fall.

The lake herring, *Coregonus artedi* LeSueur, occurs in all of the Great Lakes and in the deeper inland waters of the St. Lawrence River, Hudson River, and Mississippi River drainages (Hubbs and Lagler, 1947). The name "lake herring"

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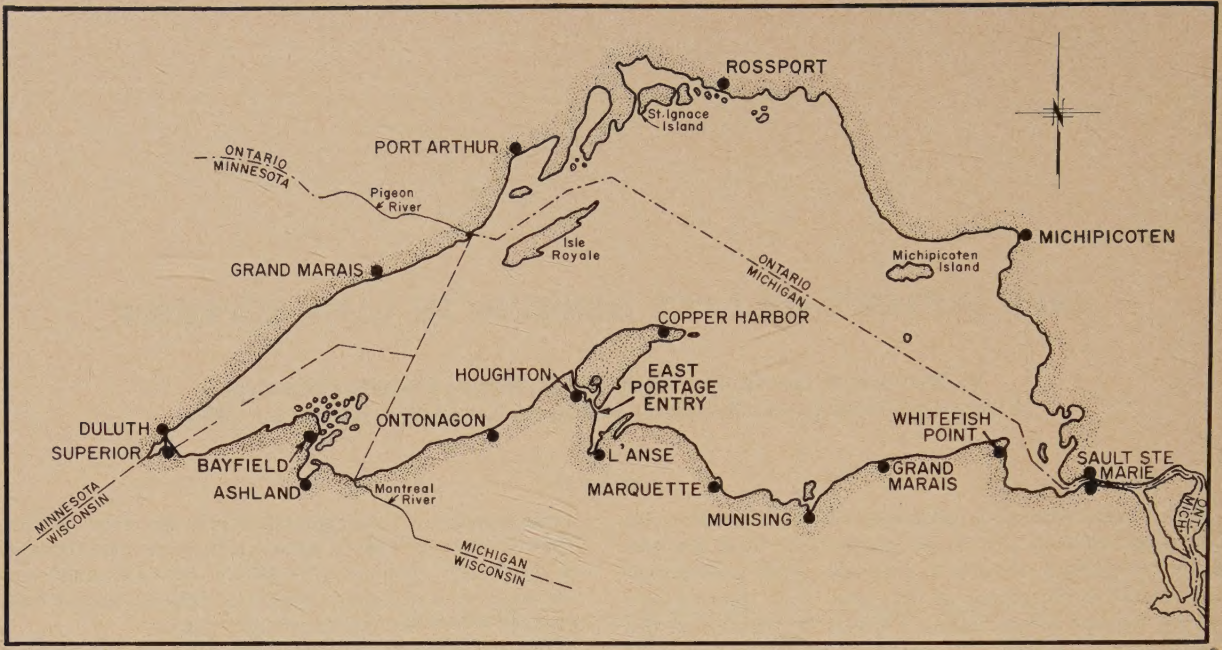
ROSSPORT
St. Ignace Island
PORT ARTHUR
ONTARIO
MINNESOTA
Pigeon River
Isle Royale
GRAND MARAIS
MICHIPICOTEN
Michipicoten Island
ONTARIO
MICHIGAN
COPPER HARBOR
HOUGHTON
EAST PORTAGE ENTRY
DULUTH
SUPERIOR
BAYFIELD
ONTONAGON
ASHLAND
Montreal River
L'ANSE
MARQUETTE
MUNISING
GRAND MARAIS
WHITEFISH POINT
SAULT STE MARIE
MINNESOTA
WISCONSIN
MICHIGAN
WISCONSIN

Figure 1.—Map of Lake Superior.

undoubtedly originates from the resemblance and analogous ecological position to the Atlantic marine herring, *Clupea harengus*. Both are pelagic and feed largely on plankton. They are the basis of considerable commercial fishing and also serve as forage for the more valuable food fishes—the marine forms for cod and other predators, and the fresh-water forms for the once-abundant lake trout.

The lake herring did not gain high importance in the Great Lakes fisheries until the early 1900's when it assumed first position in the total Great Lakes production; it has held this rank to the present time. The average production in U.S. waters in 1929–61, the most recent years for which dependable statistics are available for all Great Lakes, was nearly 19 million pounds. The catch of 24,371,000 pounds in 1948 was the highest recorded in that period, but Lake Erie alone produced greater catches before the collapse of the fishery there in 1925. Production in the Great Lakes in most recent years has not equalled that of the earlier years, but continues to be substantial (nearly 21 million pounds, for example, in 1954).

The lake herring (usually known as cisco in Lake Erie and in small lakes) is a member of an extremely complex genus. The coregonines have confused taxonomists for many decades, and even though researchers have added greatly to the amount of data available, the group is still not well understood. The confusion stems from the difficulty in describing a group which varies widely in size, shape, and systematic characters, and in which the morphology is affected by the environment. The deepwater members of the genus, known collectively as chubs, are often difficult and sometimes impossible to identify by species at the smaller sizes. The separation of lake herring from chubs, however, rarely causes difficulty.

Numerous papers have been published on the age, growth, and ecology of *C. artedi* of the smaller lakes but the only major publications on the species in the Great Lakes have been those of Van Oosten (1929), Scott (1951), and Smith (1956). This paper is the first contribution to the life history of the lake herring in Lake Superior.

MATERIALS AND METHODS

The studies of the Lake Superior lake herring were based on 12,187 specimens collected from commercial and experimental gill nets fished at various locations and dates during 1950–62. The main study of age and growth was based on 3,779

TABLE 1.—*Ports and dates of collection of Lake Superior lake herring used in study of age and growth*

Date	Port	Gill net mesh size	Number of fish
1950		*inches*	
Dec. 4	Bayfield	(1)	103
Dec. 5	Portage Entry	(1)	96
Dec. 15	Marquette	2½	68
1951			
Nov. 20	Marquette	2⅜	106
Nov. 27	Bayfield	2⅜	147
Nov. 27	Portage Entry	2⅜	123
1952			
Nov. 11	Bayfield	2⅜	125
Nov. 24	Portage Entry	2⅜	106
Dec. 11	Marquette	2⅜	101
1953			
Nov. 20	Marquette	2⅜	84
Dec. 1	Portage Entry	2⅜	91
1954			
Dec. 1	Portage Entry	2½	96
Dec. 6	Bayfield	2¼	161
Dec. 10	Marquette	2½	102
1955			
Dec. 2	Portage Entry	2⅜	85
Dec. 5	Marquette	4½	95
1956			
Nov. 6	Marquette	2⅜	72
Nov. 11	Portage Entry	2⅜	143
Nov. 19	Bayfield	2⅜	93
Dec. 5	Marquette	2⅜	83
Dec. 10	Portage Entry	2⅜	100
1957			
Nov. 25	Portage Entry	2⅜	106
Nov. 26	Marquette	2⅜	81
Nov. 27	Bayfield	2¼	105
Dec. 3	Duluth	(1)	47
Dec. 4	Bayfield	2¼	92
Dec. 6	Duluth	(1)	43
Dec. 9	Portage Entry	2⁷⁄₁₆	103
Dec. 9	Marquette	2⁷⁄₁₆	78
1958			
Nov. 25	Portage Entry	2⁷⁄₁₆	118
Dec. 1	Marquette	2⅝	117
Dec. 3	Duluth	2¼–2½	122
Dec. 10	Bayfield	2½	116
1959			
Nov. 24	Duluth	2⅜	113
Dec. 1	Portage Entry	2⅜–2½	125
Dec. 1	Marquette	2½	123
Dec. 8	Bayfield	(1)	110
Total			3,779

[1] Mesh size unkown.

fish from commercial landings at: Duluth, Minn.; Bayfield, Wis.; and Portage Entry and Marquette, Mich., (fig. 1) during the fall spawning seasons of 1950–59 (table 1). The mesh sizes of the commercial gill nets ranged from 2¼ to 2⅝ inches, extension measure (the sample collected at Marquette in 1955 came from 4½-inch-mesh trout nets). The 2⅜-inch-mesh gill nets were by far the most common in the fishery. Scale samples and data on length, weight, sex, and state of gonads were obtained from each fish.

The remainder of the samples came from experimental gill nets fished from the Bureau's research vessel *Siscowet* (fig. 2) in western Lake Superior (table 2), from special collections during the 1961 spawning run at Bayfield, and from the summer lake herring fishery at Marquette. The numbers of fish employed in the individual phases of the life-history study varied according to the appropriate materials available or the number of specimens required. The numbers and sources of the fish used for each particular study are listed n the text.

All collections used in this report represent the entire catch or net-run samples.

Total length (tip of the snout to the end of the tail, lobes compressed) was recorded to the nearest 0.1 inch. Weights were measured on a spring scale and recorded to the nearest 0.1 ounce. All lengths are given in inches, and weights in ounces.

Whenever possible, the scales for the study of age and growth were removed from the left side of the body at a point midway between the lateral

TABLE 2.—*Lake herring taken in experimental gill nets by the M/V* Siscowet *in western Lake Superior, 1958–61*

Date	Number of fish
1958	
June	323
July	62
August	45
September	774
October	53
November	208
December	80
1959	
April	6
May	23
June	9
July	289
August	4
September	32
October	177
November	886
December	272
1960	
April	66
May	57
June	20
July	53
September	176
October	217
November	269
December	621
1961	
May	2
June	5
July	6
September	120
October	10
November	245
December	74
Total	5,184

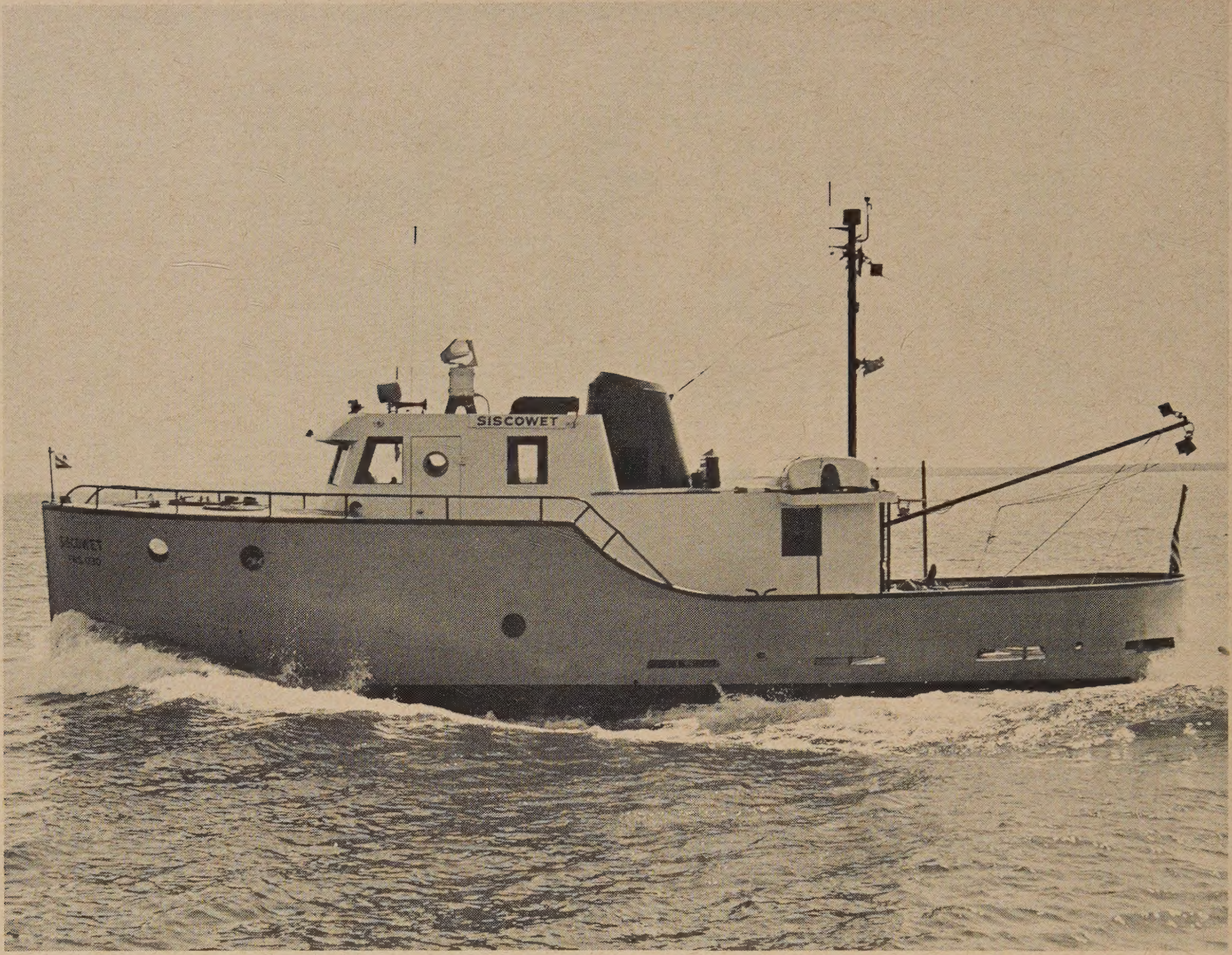

FIGURE 2.—M/V *Siscowet.*

line and the middle of the base of the dorsal fin. Scales were not always available from this area, however, particularly on fish which had been choked through the gill nets, thus leaving them devoid of scales in the midriff. Under these circumstances, the scales were removed from wherever they could be found, usually from a point posterior to the dorsal fin.

Plastic impressions of scales were made in cellulose acetate (Smith, 1954) and were magnified 43 diameters by means of a microprojector (Moffett, 1952). Diameters of scales and growth fields were measured through the focus along a line that roughly bisected the anterior field, and were recorded to the nearest millimeter.

Some difficulty was encountered in distinguishing accessory marks or false annuli from the true annuli. If doubt as to true age was great, the specimen was excluded from the analysis. It is felt that these few exclusions (about 3 percent) made the age determinations reasonably dependable.

Age groups are designated by Roman numerals corresponding to the number of annuli. All the fish were considered to have passed into the next age group on January 1. For fish of all spawning-run collections, the numbers of completed growing seasons ran one greater than the indicated ages. The annulus formation offered no difficulties in age determinations since the samples for the age and growth studies were all collected during the fall spawning run, whereas the annulus is laid down in the early summer.

Calculations from scale measurements of lengths at time of completion of earlier annuli were made by direct proportion. The validity of this method was demonstrated for Saginaw Bay (Lake Huron) lake herring by Van Oosten (1929) and for Green Bay (Lake Michigan) lake herring by Smith (1956). Materials available in the present study were unsuitable for the determination of the body-scale relation for lake herring of Lake Superior.

An instructive discussion of the various phases of this paper requires a preliminary statement on the probable extent to which various sources of bias affect the data. The major bias to the data from the spawning-run samples can be traced to four sources: gear selection; segregation on the basis of maturity; selective fishing mortality; and time of capture within the spawning season. These sources may act independently or collectively to prejudice estimates of age composition, relative strength of the year classes, size at capture, growth, sex composition, and annual fluctuations in size and growth. The first two factors have so much in common that certain of their effects cannot be separated, and together they make possible the selective fishing that leads to the progressive change in the actual growth of the survivors.

Bias from gear selection affects estimates of age composition through failure of the gear to take representative samples of the younger age groups which actually may be present on the spawning grounds. The selection of only the larger members of the younger age groups causes overestimates of average size and calculated lengths. The possibility of selecting the small members of the older age groups also exists, but the scarcity of old fish and the reduction of growth with age probably make this selection insignificant. Changes from cotton to nylon twine, in mesh sizes, and subtle changes in the hang of the net may bias comparisons among samples, especially those dealing with changes in the average size, growth, and weight. During 1950–55 the 2⅜-inch-mesh net was the most common, although samples were collected from 2½-inch-mesh nets in Marquette in 1950 and 1954 and at Portage Entry in 1954. One sample was collected from 2¼-inch-mesh nets at Bayfield in 1954. In the years following 1955, the fishery adjusted the mesh size to conform with the increased size of the fish at all ports except Bayfield (comparable data are not available for Duluth). At Portage Entry, the 2 7/16- and 2½-inch-mesh nets were in common use, and at Marquette the mesh sizes ranged from 2⅜-inch in 1956 to 2⅝-inch mesh in 1958, 1960, and 1961. At Bayfield, despite the increased size of the fish, the mesh sizes actually decreased during 1956–61 from 2⅜- in 1956 to 2 5/16-inch mesh in 1961.

Successively larger meshes would be expected to capture fish of larger size, and the shorter fish captured should have a greater relative girth (and hence, be heavier than fish of the same length captured in nets with smaller meshes). Deason and Hile (1947) found that *C. kiyi* of the same length captured in nets of successively larger meshes had successively greater values of the coefficient of condition, *K*.

Other questions arise relating to comparisons among samples taken from different makes of twine. The mesh sizes recorded in the data were those ordered by the fishermen and not necessarily the actual size as fished. Different twine companies supply different mesh sizes on identical orders; some produce mesh sizes which are scant whereas others give accurate meshes. Also, lots of twine of the same general material (e.g., cotton, linen, or nylon) have different shrinkage under use. When the fisherman receives the twine he may hang the net on the one-half basis (i.e., 4 feet of twine, flat mesh, hung on 2 feet of maitre) or tighter, such as two-third basis (6 feet of twine on 4 feet of maitre). The selective action of the gill nets may vary according to their hang—a tightly hung net has a lesser tangling action and hence may be more selective than one hung loosely.

Undoubtedly the most severe source of bias in the spawning-run collections was segregation on the basis of maturity. Since only mature individuals were found on the spawning grounds, I-group fish were entirely lacking and age groups II and III were poorly represented. Age group IV was the first age at which all of the lake herring were mature; consequently, fish of this age group were persistently dominant in the samples. Only the faster growing of the younger age groups were mature. Bias from segregation according to maturity is made more complicated by sex differences in attainment of maturity. Since females mature at a greater size and age than do males, overestimates of growth and underestimates of numbers among younger fish are more severe for them. Data on sex ratio by age are impaired correspondingly.

The production of about 90 percent of the annual catch under the conditions just described leads to selective fishing mortality according to growth rate and sex. This selective destruction modifies the growth and sex ratio of a year class as it passes through the fishery. At the younger ages males are subjected to greater mortality than females, and the faster growing fish of both sexes are eliminated. The survivors of a year class have slower growth, and fewer males than would be characteristic of a year class which had not been subjected to a selective fishery or to no fishery at all. In some situations the longer exposure of males to selective fishing could make them appear to grow more slowly than females whether or not the sexes actually grew at different rates. The selective destruction probably does not end until all of the fish are mature and fully vulnerable to the gear.

Records of age composition and hence also judgments of year-class strength may be affected by the time of capture within the spawning season. Collections made in the early days of the season often had an unduly high percentage of fish in the younger age groups (the early-maturing males of the population reach the spawning grounds first). Conversely, samples collected during the last few days of the season frequently included disproportionately large numbers of fish in the older age groups (see section on reproduction). This source of bias is most damaging at the extremes of the season—the time of capture is of little consequence during the main season.

COMMERCIAL FISHERY FOR LAKE HERRING

The lake herring has been the principal species in the commercial production in U.S. waters of Lake Superior since 1908 (Koelz, 1926). Between 1891 and 1907 the lake trout occupied first place in poundage produced, and in the years prior to 1891 the whitefish was the principal species taken.

The statistical records of lake herring production in Lake Superior for 1929–61 (table 3) are from Lake Fish issued annually by the Bureau of Commercial Fisheries and those for Ontario are issued by the Province.

The first published record of lake herring production in Lake Superior is for 1867 in Ontario. The first record of production in the U.S. waters of Lake Superior is for 1879, but in 1879–1928 the statistics often included the catch of small chubs and in some years the catch of round whitefish (*Prosopium cylindraceum*). Only since about 1929 can the records for lake herring production in the U.S. waters of Lake Superior be termed reasonably dependable.

TABLE 3.—*Production (thousands of pounds) of lake herring in Lake Superior, 1929–61*

Year	United States				Canada	Grand total
	Minnesota	Wisconsin	Michigan	Total	Ontario	
1929	8,571	2,625	1,516	12,712	2,529	15,241
1930	8,368	705	2,341	11,414	2,745	14,159
1931	5,363	662	886	6,912	1,396	8,308
1932	5,123	362	540	6,026	962	6,988
1933	5,203	650	941	6,794	1,744	8,538
1934	8,017	2,946	2,068	13,031	2,157	15,188
1935	7,911	2,422	2,782	13,115	1,506	14,621
1936	5,243	2,856	3,657	11,757	2,789	14,546
1937	5,623	2,991	3,170	11,784	2,378	14,162
1938	5,715	2,485	2,394	10,594	1,917	12,511
1939	6,590	3,119	3,357	13,066	1,435	14,501
1940	7,381	4,909	4,213	16,502	1,201	17,703
1941	5,724	6,160	5,954	17,838	1,433	19,271
1942	4,697	5,035	5,113	14,844	1,393	16,237
1943	5,079	4,435	4,360	13,874	1,209	15,084
1944	5,069	4,712	4,446	14,227	1,481	15,708
1945	4,398	6,538	3,109	14,045	1,708	15,753
1946	3,443	6,342	3,357	13,142	1,511	14,653
1947	2,904	4,641	3,263	10,808	1,017	11,825
1948	3,890	6,291	4,524	14,705	1,285	15,991
1949	4,054	5,028	4,122	13,204	1,255	14,459
1950	2,489	3,953	1,715	8,158	505	8,663
1951	2,249	5,347	2,829	10,424	763	11,187
1952	2,683	5,890	3,448	12,021	993	13,014
1953	2,667	5,356	2,415	10,439	745	11,184
1954	2,854	5,575	3,393	11,823	920	12,743
1955	2,332	4,359	3,443	10,134	708	10,842
1956	2,600	4,158	3,719	10,478	821	11,299
1957	3,177	3,162	5,017	11,355	1,696	13,051
1958	2,870	2,496	4,850	10,216	1,744	11,960
1959	2,408	2,862	6,242	11,512	2,833	14,345
1960[1]	1,863	2,255	6,693	10,806	2,117	12,923
1961[1]	1,580	2,559	7,306	11,445	1,505	12,950

[1] Materials supplied for this report in advance of general release for all species.

Lake Superior contributed an average of 62.4 percent to the total U.S. production of lake herring for the Great Lakes in 1929–59. (This percentage unquestionably was much lower before the collapse of the highly productive Lake Erie cisco fishery in 1925.) The annual percentage contribution ranged from 39.7 percent in 1931 to 92.0 percent in 1959. The high figure for 1959 did not reflect a particularly great yield in Lake Superior but rather a very low catch of lake herring in the other Great Lakes.

In the U.S. waters of Lake Superior the catch of lake herring was 12.7 million pounds in 1929, dropped to 6 million pounds in 1932, and reached nearly 18 million pounds in 1941, the highest production recorded. Since 1934 the take has exceeded 10 million pounds in all years but one (1950).

Although the catch of lake herring has contributed nearly three-fourths (74.2 percent) to the 1929–59 total U.S. production of Lake Superior, the value of the lake herring represented less than one-third (30.4 percent) of the total. The annual percentage contribution to the total value of the fishery ranged from 17.7 percent ($67,000) in 1932 to 56.9 percent ($854,000) in 1941. In recent years the lake herring has contributed a relatively high percentage to the total value of the fishery due to the drastic decline of the high-priced lake trout.

Reasons for the relatively low value of the lake herring stem from strongly seasonal production, capture and handling procedures, and technological problems. On the average, about 90 percent of the annual production occurs during the November-December spawning run when the market is soon glutted. Individual catches, often running as large as 10 tons, are piled in the gill net tugs and brought to shore where they are picked from the nets in warm sheds. Little care is taken in picking the fish from the nets. The rough treatment of this highly palatable but delicate fish often produces an inferior product hardly fit for human consumption. Even those fish which are removed carefully from the nets and well iced soon become soft and unappetizing. Frozen lake herring readily dehydrate and suffer objectionable oxidation of the fat.

In the early years, nearly all of the lake herring were salted; large quantities were shipped to economically depressed areas in the east and southeast. With the advent of mink farming in the early 1940's, a large percentage of the lake herring was sold for mink food. The 1961 lake herring production at Bayfield, Wis., was divided about equally between salt herring and mink food.

The distribution of the catch of lake herring among the different states has shifted markedly during the period for which sound statistics are available. Minnesota dominated the catch in 1929–40, Wisconsin held the lead in 1941–56 (exception was 1942 when Michigan occupied first place), and Michigan had the largest catch in 1957–61.

The 1929–61 average annual production of lake herring from Canadian waters of Lake Superior was 1,527,000 pounds, only 11 percent of the lake's total. The catch exceeded 2 million pounds in only 7 years and was below 1 million in 8 years.

TABLE 4.—*Average catch (pounds) of Lake Superior lake herring per 1,000 feet of gill nets lifted in November–December 1929–59*

[Number of feet of nets lifted (in thousands of feet) is in parentheses]

Year	Minnesota	Wisconsin	Michigan[1]
1929	---------	---------	303 (3, 235)
1930	---------	---------	248 (5, 656)
1931	---------	---------	170 (8, 830)
1932	---------	---------	175 (2, 421)
1933	---------	---------	186 (3, 549)
1934	---------	---------	194 (7, 326)
1935	---------	---------	205 (8, 709)
1936	---------	---------	226 (12, 182)
1937	---------	---------	155 (15, 831)
1938	---------	---------	165 (11, 901)
1939	---------	---------	164 (18, 110)
1940	---------	---------	264 (13, 092)
1941	---------	---------	266 (17, 909)
1942	---------	---------	230 (16, 676)
1943	---------	---------	206 (15, 735)
1944	---------	---------	232 (13, 210)
1945	---------	---------	216 (13, 006)
1946	---------	---------	282 (9, 854)
1947	---------	---------	173 (15, 900)
1948	---------	---------	279 (13, 815)
1949	268 (8, 906)	688 (7, 086)	330 (11, 128)
1950	286 (5, 240)	490 ---------	224 (6, 714)
1951	352 (4, 100	745 (7, 100)	395 (6, 783)
1952	348 (5, 343	765 (7, 566)	445 (6, 293)
1953	444 (3, 217)	670 (7, 901)	396 (4, 995)
1954	320 (4, 697)	542 (10, 217)	449 (6, 699)
1955	303 (4, 439)	641 (6, 749)	469 (5, 812)
1956	330 (3, 996)	665 (6, 101)	409 (6, 267)
1957	317 (4, 944)	483 (6, 370)	419 (9, 811)
1958	301 (4, 038)	472 (5, 172)	356 (9, 738)
1959	218 (4, 940)	424 (6, 590)	295 (14, 517)
1960	190 (3, 076)	548 (3, 825)	299 (13, 033)
1961	192 (3, 760)	715 (3, 331)	345 (11, 739)
Average 1949–61	298 (4, 669)	604 (6, 501)	372 (8, 733)
1929–61	---------	---------	278 (10, 317)

[1] Based on the November–December catch per unit effort for statistical districts 1–4 and 6. To obtain the grand averages in the column, the catch per unit effort in each district was weighted by the percentage contribution of the district to the total State of Michigan catch in 1929–43.

Although recent production of lake herring in U.S. waters is not significantly below that of the 1929–61 mean of 11,794,000 pounds, some evidence exists that the abundance has declined in certain areas of the lake, particularly in Minnesota. The catch per unit effort during the 2-month spawning season in Minnesota (table 4) reached a peak of 444 pounds per 1,000 linear feet of net lifted in 1953, but the trend was downward after that year and the 1960–61 catch per unit effort (mean of 191 pounds) was the lowest for the 13-year period. Much of the decline in Minnesota can be traced to the near collapse of the fishery in the Duluth area, which in the years prior to 1955, contributed the major portion of Minnesota's production. The average annual catch per unit effort at Duluth in 1951–53 was over 300 pounds. An erratic decline in abundance after 1953 reduced the catch per unit effort to only 68.5 pounds in 1960 (the catch per unit effort increased slightly to 91.7 pounds in 1961).

TABLE 5.—*Average catch of Lake Superior lake herring per 1,000 linear feet of gill nets lifted in November-December, 1950–59, according to weight and number of fish*

Year	Minnesota [1]		Wisconsin[1]		Portage Entry		Marquette	
	Number of pounds	Number of fish	Number of pounds	Number of fish	Number of pounds	Number of fish	Number of pounds	Number of fish
1950	--------	--------	490	1,307	200	471	265	643
1951	--------	--------	745	2,055	426	1,082	325	722
1952	--------	--------	765	1,826	462	1,001	472	967
1953	--------	--------	--------	--------	421	999	320	656
1954	--------	--------	542	1,262	504	1,320	213	425
1955	--------	--------	--------	--------	519	1,154	273	588
1956	--------	--------	665	1,565	451	949	242	471
1957	317	757	483	991	453	928	330	468
1958	301	669	472	995	381	664	269	439
1959	218	425	424	807	305	554	267	442
1960	190	380	548	913	313	538	271	434
1961	--------	--------	715	1,395	334	534	431	651
Average:								
1950–55	--------	--------	636	1,613	422	1,005	311	667
1956–61	--------	--------	551	1,111	372	695	302	484
Percentage decrease	--------	--------	13.4	31.1	11.8	30.8	2.9	27.4

[1] Data were lacking to calculate the numerical catch per unit effort for Minnesota in 1950–56 and for Wisconsin in 1953 and 1955.

Some evidence of declining abundance exists also in Wisconsin waters where the catch per unit effort during the 2-month spawning season declined from a mean of 649 pounds per 1,000 feet of gill nets lifted in 1949–55 to 551 pounds in 1956–61. The catch per unit effort in 1961 (715 pounds), however, was the highest since 1952 (765 pounds). On the other hand, little evidence of a decline exists in those Michigan waters in which substantial catches were made each year since 1929. The average catch per 1,000 feet of gill nets in 1956–61 (354 pounds) was slightly below that of 1949–55 (387 pounds), but far above the 1929–61 mean of 278 pounds.

A measure of abundance according to numbers of fish caught per unit effort, rather than pounds of fish, may better describe changes in population density. Since the average size of the lake herring captured was greater in 1956–61 than in 1950–55, fewer individuals were required to reach the same weight in the later period. The data are inadequate to make comparisons between the early and late periods at Duluth since samples were taken only in 1957–60. The catch per unit effort in pounds at Bayfield declined 13.4 percent from 1950–55 to 1956–61 (table 5). The catch per unit effort in numbers,[1] on the other hand, declined 31.1 percent (from 1,613 in 1950–55 to 1,111 in 1956–61). The decrease in catch per unit effort according to weight from the early to the later period was 11.8 percent at Portage Entry and 2.9 percent at Marquette. The number of fish caught per 1,000 feet of gill nets lifted decreased 30.8 percent at Portage Entry and 27.4 percent at Marquette.

Fishing effort, based on the number of linear feet of gill nets (in units of 1,000 feet) lifted during the 2-month spawning season, varied from state to state and year to year (table 4). Fishing effort in Minnesota ranged from 3,076 units in 1960 to 8,906 units in 1949 (the 1949–61 mean was 4,669). The fishing effort in Wisconsin exceeded that of Minnesota in all years except two (1949 and 1961). The number of units exceeded 10,000 in 1954, and the 1949–61 mean was 6,501. Fishing effort in Michigan[2] exceeded 10,000 units lifted in 1936–49 (exception in 1946 when the value was 9,854 units) and in 1959–61. Over 18,000 units of gill nets were lifted during the 2 spawning months in 1939. The 1949–61 mean was 8,733 units, well below the 1929–61 average of 10,317.

The interpretation of data on catch per unit effort for lake herring in terms of actual availability is difficult because of the recent changeover from cotton to nylon gill nets. This change took place much later and at a slower pace in Lake Superior than did the changeover to nylon trout nets. Not until 1958 or 1959 were the majority of Wisconsin lake herring fishermen using nylon nets, and a few fishermen were still fishing cotton nets in 1961. Since the cotton lake herring nets were commonly used only once a year, during the fall spawning season, they lasted many years. The fishermen were reluctant to replace perfectly good cotton nets with new, expensive nylon.

Extensive observations on the relative efficiency of cotton and nylon lake herring nets have not been made. The Bureau's research vessel *Cisco* provided comparisons between the catch of chubs in nylon and linen gill nets in Lake Michigan. Nylon gill nets took 2.2 times as many chubs as linen nets of corresponding mesh fished in the same gang. The Bureau vessel *Siscowet* obtained only one comparison between catches of lake herring in nylon and cotton nets. In this experiment the nylon nets took 4.3 times as many lake herring as did cotton nets fished in the same gang.

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[1] The numerical catch per unit effort was based on the catch per unit effort in pounds divided by the average weight of the fish in the sample.

[2] Total November–December effort for statistical districts 1–4 and 6.

Since the conversion to nylon nets has taken place slowly over the past 5 to 8 years and dependable conversion factors on the relative efficiency of the two types of nets for taking lake herring are unavailable, it appears impossible to undertake any adjustment in the statistics. Fishing intensity, therefore, may have been underestimated and the availability or abundance, based on the catch per unit effort, may have been to the same degree overestimated more and more as nylon nets replaced cotton nets.

ANNULUS FORMATION AND PROGRESS OF THE SEASON'S GROWTH

Smith (1956) determined that some lake herring started new growth in Green Bay as early as May 8 in 1950, and that annulus formation was completed by July 13. Van Oosten (1929) suggested that annulus formation occurred during the winter for the lake herring of Saginaw Bay.

Information on the time of annulus formation is scarce from Lake Superior since lake herring were difficult to catch during the spring and early summer. The only reliable data came from Marquette where an early-summer lake herring fishery developed in 1961 and continued in 1962.

The earliest collection was made on May 3, 1962 (table 6), and included several fish which had already begun new growth. As late as July 27 (a full 2 weeks after annulus formation was completed in Green Bay), a few individuals still gave no indication of new growth. New growth had started on all of the lake herring collected on August 21, 1961, and on all fish collected later that season.

Among the best represented age groups (IV–VI), the younger fish started new growth earlier than did the older ones. On June 28, for example, 94 percent of the IV-group and 86 percent of the V-group fish had a completed annulus as contrasted with a percentage of 65 for age group VI. On July 27, the percentages were 100 and 96 for age groups-IV and V but only 88 percent for VI-group fish.

TABLE 6.—*Percentage of lake herring with completed annuli collected at Marquette during period of annulus formation*

[Number of fish in parentheses]

Date	Percentage with completed annuli in age group						Ages combined
	III	IV	V	VI	VII	VIII	
1962							
May 3	17 (46)	11 (101)	8 (109)	0 (70)	5 (22)	0 (4)	8 (352)
1961							
June 28	50 (4)	94 (16)	86 (20)	65 (17)	64 (11)	20 (5)	73 (73)
July 27	88 (8)	100 (21)	96 (25)	88 (25)	60 (5)	75 (4)	91 (88)
Aug. 28	100 (14)	100 (26)	100 (27)	100 (12)	100 (6)	-------- --------	100 (85)

The period of annulus formation for lake herring in Lake Superior exceeds 8 weeks. Extreme care is needed in age determination for fish captured during the spring and early summer.

The data on the amount and percentage of the season's growth were taken from samples collected at Marquette during the summer of 1961 and in the spring of 1962 (table 7). Collections were not available in 1961 until late June when the summer fishery started. Since the summer fishery ended in late September, the estimate of full season's growth was based on samples of the same year class collected in May 1962. Special arrangements were made to obtain these samples before the regular summer fishery began in late June.

The records of table 7 exhibit some irregularities in trend which probably can be attributed to the small numbers of fish on which certain estimates were based. Ten of 29 estimates were based on fewer than 10 fish. The most reliable data are those for age groups IV, V, and VI, where all 15 percentages are based on more than 10 fish and 12 on 20 or more.

Despite the irregularities in the data, a general idea of the progress of the season's growth can be formed from the weighted means of the percentages of growth completed for the different dates (fig. 3).

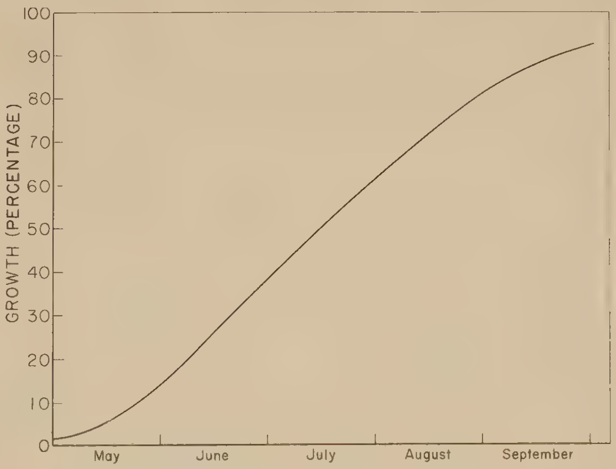

FIGURE 3.—Percentage of season's growth completed at time of capture, age groups combined. The curve was drawn freehand on the basis of data of table 7.

TABLE 7.—*Amount of season's growth in length (inches) completed by age groups on various dates of capture*

[The full season's growth of fish caught in 1961 determined from samples of the same year class collected on May 3, 1962]

Age group and item	Date of collection					Full-season growth in 1961
	May 3, 1962 [1]	June 28, 1961	July 27, 1961	August 21, 1961	September 25, 1961	
Age group III:						
Current-season growth	0.08	0.19	0.76	1.16	1.09	1.58
Percentage completed	5.1	12.0	48.1	73.4	69.0	100.0
Number of fish	46	4	8	14	5	77
Age group IV:						
Current-season growth	0.04	0.47	0.84	1.07	1.15	1.28
Percentage completed	3.1	36.7	65.6	83.6	89.8	100.0
Number of fish	101	16	21	26	20	184
Age group V:						
Current-season growth	0.02	0.35	0.68	0.83	0.99	0.96
Percentage completed	2.1	36.5	70.8	86.5	103.1	100.0
Number of fish	109	20	25	27	26	207
Age group VI:						
Current-season growth	0.00	0.42	0.51	0.63	0.82	0.89
Percentage completed	0.0	47.2	57.3	70.8	92.1	100.0
Number of fish	70	17	25	12	14	138
Age group VII:						
Current-season growth	0.01	0.42	0.33	0.56	0.49	0.79
Percentage completed	1.3	53.2	41.8	70.9	62.0	100.0
Number of fish	22	11	5	6	5	49
Age group VIII:						
Current-season growth	0.00	0.04	0.39	----------	0.85	0.85
Percentage completed	0.0	4.7	45.9	----------	100.0	100.0
Number of fish	4	5	4	----------	2	15
Average percentage: [2]						
All age groups	2.3	38.0	60.9	80.1	92.0	100.0
Age groups III–V	3.0	34.1	65.4	82.6	94.5	100.0
Age groups VI–VIII	0.3	42.8	53.7	70.8	85.8	100.0

[1] Current-season growth made in 1962; percentage computed from full-season growth of fish of same age in 1961.

[2] Weighted means.

The following percentages were obtained from the curve in the same figure:

Period of growth	Percentage of season's growth completed	
	During period	At end of period
Before May	2.3	2.3
May	11.5	13.8
June	25.0	38.8
July	22.5	61.3
August	20.0	81.3
September	11.2	92.5
After September	7.5	100.0

The greatest amount of growth in any single month took place in June (25.0 percent) and by the end of August, 81.3 percent of the season's growth was completed. Over two-thirds of the season's growth was in June–August and 90 percent in May–September.

Growth of Green Bay lake herring started sometime in May and ended in October (Smith, 1956). The greatest amount of growth took place in July. Hile (1936) found that growth of lake herring (ciscoes) in northeastern Wisconsin was complete by the end of July in Trout Lake, near the end of August in Muskellunge Lake, in early September in Sliver Lake, and in early October in Clear Lake. Differences in the length of the growing season contributed importantly to differences of growth rate in the four populations.

Growth of the related *C. kiyi* of northern Lake Michigan (Deason and Hile, 1947) was 39 percent completed by June 14, 80 percent by July 9, and 100 percent completed by September 7.

AGE COMPOSITION AND YEAR-CLASS STRENGTH

AGE COMPOSITION

The age composition of the spawning-run samples varied relatively little from year to year and port to port. Age group IV dominated the catch in each year's collection at each port. Indeed, the contribution of the IV group (table 8) exceeded 50 percent in all but 8 collections (Duluth, 1957 and 1959; Bayfield, 1958; Portage Entry, 1955 and 1958; and Marquette, 1955, 1956, and 1959). The highest percentage of IV-group fish was 68.1 (Bayfield, 1957) and the lowest was 37.0 percent (Bayfield, 1958). The average percentage for the IV group for the combined collections was 53.2.

Fish of age group III were second in abundance in 16 of the 31 collections. The percentage contribution ranged from 11.0 (Bayfield, 1959) to 40.6 (Portage Entry, 1954) and averaged 24.8. The V

Table 8.—*Age composition of Lake Superior lake herring according to port and year of capture*

[Averages are unweighted]

Port and year of capture	Number of fish	Percentage age group						Average age
		II	III	IV	V	VI	VII	
Duluth:								*Years*
1957	90	5.6	15.6	42.2	34.4	2.2	------	4.1
1958	122	2.5	31.1	50.8	15.6	------	------	3.8
1959	113	0.9	21.2	37.1	24.8	14.2	1.8	4.4
Average	--------	3.0	22.6	43.4	24.9	5.5	0.6	4.1
Bayfield:								
1950	103	------	37.9	61.1	1.0	------	------	3.6
1951	147	------	26.5	60.6	12.9	------	------	3.8
1952	125	------	19.2	55.2	22.4	3.2	------	4.1
1954	161	------	16.8	66.5	16.1	0.6	------	4.0
1956	93	2.2	16.1	58.0	23.7	------	------	4.0
1957	197	3.0	20.8	68.1	8.1	------	------	3.8
1958	116	5.2	24.1	37.0	27.6	5.2	0.9	4.0
1959	110	2.7	11.0	59.1	24.5	1.8	0.9	4.2
Average	--------	1.6	21.6	58.3	17.0	1.3	0.2	3.9
Portage Entry:								
1950	96	------	31.2	61.5	7.3	------	------	3.7
1951	123	0.8	18.7	56.1	22.8	1.6	------	4.1
1952	106	0.9	20.8	54.8	22.6	0.9	------	4.0
1953	91	3.3	39.6	53.8	3.3	------	------	3.6
1954	96	4.2	40.6	52.1	3.1	------	------	3.5
1955	85	------	20.0	43.5	34.1	2.4	------	4.2
1956	243	2.1	35.8	56.3	5.8	------	------	3.6
1957	209	3.8	22.5	58.9	14.8	------	------	3.8
1958	118	0.8	22.0	39.9	36.5	0.8	------	4.1
1959	125	1.6	14.4	54.4	28.0	1.6	------	4.1
Average	--------	1.8	26.6	53.1	17.8	0.7	------	3.9
Marquette:								
1950	68	1.5	22.1	63.2	13.2	------	------	3.9
1951	106	0.9	19.8	59.5	19.8	------	------	4.0
1952	101	------	20.8	53.4	23.8	2.0	------	4.1
1953	84	------	38.1	52.4	8.3	1.2	------	3.7
1954	102	1.0	19.6	57.8	20.6	1.0	------	4.0
1955	95	2.1	21.1	41.0	34.7	1.1	------	4.1
1956	155	3.9	27.1	44.5	21.9	2.6	------	3.9
1957	159	4.4	28.9	55.4	9.4	1.9	------	3.8
1958	117	6.0	31.6	52.1	10.3	------	------	3.7
1959	123	1.6	34.1	43.2	19.5	1.6	------	3.9
Average	--------	2.1	26.3	52.3	18.2	1.1	------	3.9
Grand total or average	3,779	2.0	24.8	53.2	18.4	1.5	0.1	3.9

group ranked second in 14 collections; it ranged from 1.0 percent (Bayfield, 1950) to 36.5 percent (Portage Entry, 1958), and averaged 18.4 percent for the combined collections. Age groups III and V were equally represented in the 1951 Marquette collection. Other age groups were sparsely represented or entirely lacking. The youngest fish were members of the II group (mean percentage contribution, 2.0). The VI group appeared in 18 collections (mean percentage, 1.5) but VII-group fish (the oldest in the samples) were taken only at Duluth in 1959 and at Bayfield in 1958 and 1959. The mean age ranged from 3.5 years in 1954 at Portage Entry to 4.4 years at Duluth in 1959. The mean ages of the combined years' collections from the several ports differed little—4.1 years at Duluth and 3.9 years at Bayfield, Portage Entry, and Marquette. The average age of fish taken in the 1950–55 period of relatively slow growth differed little from that of the faster growing fish captured in 1956–59.

The records of age composition according to sex (table 9) show a higher percentage contribution for females than for males in all age groups above III (exceptions were the VII group at Duluth and the IV group at Marquette). The differences in percentage contribution of the sexes were greatest at Duluth; the percentage of males in the III group was twice that of the females, and the percentage of females was slightly larger than that of the males in age group IV. The percentage of females was twice that of males in age group V and nearly four times in the VI group.

Table 9.—*Age composition of Lake Superior lake herring according to sex and port, 1950–59*

Port and sex	Number of fish	Percentage in age group						Average age
		II	III	IV	V	VI	VII	
Duluth:								*Years*
Males	135	6.7	33.3	42.3	14.8	2.2	0.7	3.8
Females	190	------	16.3	44.8	30.5	7.9	0.5	4.3
Bayfield:								
Males	452	2.9	26.5	55.5	14.2	0.9	------	3.8
Females	600	0.7	17.5	62.2	17.8	1.5	0.3	4.0
Portage Entry:								
Males	584	3.1	30.7	50.3	15.4	0.5	------	3.8
Females	708	1.0	23.4	57.0	17.9	0.7	------	3.9
Marquette:								
Males	701	2.1	27.5	52.2	17.3	0.9	------	3.9
Females	409	2.9	25.2	50.6	19.3	2.0	------	3.9

With few exceptions the average age of the females exceeded that of the males in each of the collections (table 10). The difference between the mean ages of the sexes among the combined collections from each port ranged from nil at Marquette to 0.5 year at Duluth.

Table 10.—*Average age of Lake Superior lake herring according to port, year of capture, and sex*

Year of capture	Duluth		Bayfield		Portage Entry		Marquette	
	Males	Females	Males	Females	Males	Females	Males	Females
1950	------	---------	3.6	3.6	3.8	3.7	3.8	4.1
1951	------	---------	3.8	3.9	4.0	4.3	4.0	4.1
1952	------	---------	4.3	4.0	3.8	4.1	4.1	4.0
1953	------	---------	------	---------	3.5	3.7	3.8	3.7
1954	------	---------	3.9	4.1	3.4	3.9	4.0	4.0
1955	------	---------	------	---------	4.1	4.3	4.1	4.3
1956	------	---------	4.0	4.7	3.5	3.7	3.8	4.0
1957	4.0	4.2	3.5	3.9	3.8	3.9	3.6	3.9
1958	3.5	4.0	3.8	4.6	4.2	4.1	3.7	3.7
1959	3.9	4.7	3.7	4.3	3.9	4.2	3.7	4.1
All years	3.8	4.3	3.8	4.0	3.8	3.9	3.9	3.9

YEAR-CLASS STRENGTH

Fluctuations in the strength of year classes of fish have been the subject of extensive research since Hjort (1914) demonstrated the significance of year-class abundance in the fluctuations of productivity of major marine fisheries. The literature in this field is so widely known and has been summarized so frequently that a review of it would not be appropriate in this paper. Even a listing of studies of year classes in the Great Lakes is not required in view of El-Zarka's (1959) broad coverage of the subject.

The evaluation of the relative strength of year classes usually has been based on data on the percentage age composition of samples in a series of years. On occasion, the records have permitted only the identification of certain year classes of unusual strength or weakness (Van Oosten and Hile, 1949—Lake Erie whitefish; Jobes, 1952—Lake Erie yellow perch). In other circumstances it has been possible to arrange year classes ordinarily (Hile, 1941—Nebish Lake rock bass) or from a series of comparisons to set up a system of "ranks" (Hile, 1954—Saginaw Bay walleye). El-Zarka (1959—Saginaw Bay yellow perch) attempted to improve the precision of estimates of year-class strength by subjecting his data on percentage age composition to an analysis of year-to-year change similar to the one used by Hile (1941) for the study of annual fluctuations of growth rate.

Instructive as these uses of data on age composition may be, much more effective judgments can be made of the strength of year classes if catch-effort data are available on the fishery from which samples were obtained. Records of catch per unit of fishing effort make it possible to estimate the availability of each age group in terms of numbers of fish. The study of fluctuations in the strength of year classes of lake herring in Lake Superior accordingly has been based on the application of age-composition data for spawning-run samples to statistics on the catch (in pounds) per 1,000 linear feet of small-mesh gill nets during the spawning months of November and December. The procedures followed are similar to those employed by Pycha (1961) in his study of the year classes of walleye in northern Green Bay, Lake Michigan. El-Zarka (1959) had recognized the value of this approach but was unable to use it because of the small numbers of legal-sized fish in certain of his samples.

The application of data on age composition to statistics on catch per unit effort is illustrated best by a hypothetical example. Let it be assumed that a sample containing 223 lake herring weighed 69.1 pounds and that the catch of lake herring of the same port in the same year was 341 pounds per 1,000 feet of gill net lifted in November and December. It is then computed that 1,000 feet of commercial nets took 341/69.1=4.935 times as many lake herring as were in the sample. Numbers per unit effort for individual age groups are then calculated by multiplying the number in the age group by the ratio 4.935; for example, an age group that contributed 43 fish to the sample was produced in the commercial fishery at the rate of 43×4.935=189 individuals per 1,000 feet of net. It was by this procedure that the records of table 11 were obtained. Data are given only for age groups III, IV, and V since other age groups were poorly represented or lacking in the samples.

Numbers of fish caught per unit effort were estimated for certain age groups as indicated by footnote in table 11. All figures for the III groups of the 1946 year class and the V groups of the 1955 year class were estimated; at Bayfield, additional estimates were needed to fill gaps created by the lack of collections in 1953 and 1955. These estimations required first the determination of the ratios of the average numbers of fish in different age groups from all available samples at a port; the appropriate ratios were then applied to available data on year classes to obtain estimates for missing data. The actual computation for age group III of the 1946 year class at Bayfield illustrates the procedure. From all available Bayfield samples it was determined that the average number of lake herring in age group III amounted to 0.378 times the average number in age group IV and 1.317 times the average number in age group V. The following two estimates then were made of the number per unit effort for the missing III group of the 1946 year class; 0.378×799=302; 1.317×265=349. The mean of the two estimates, 326, was entered in table 11. All other estimates were obtained similarly.

The relations among the succesive samples of the same year class off a port varied widely in samples from all three ports (table 11). The

TABLE 11.—*Numbers of lake herring caught per lift of 1,000 linear feet of small-mesh gill nets by year class and age group, off three Lake Superior ports*

[Based on samples from commercial landings during the spawning season and on catch-effort statistics for November and December]

Port and age group	Year class										Average
	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	
Bayfield:											
III	[1] 326	495	545	351	[1] 317	212	[1] 224	252	206	240	317
IV	799	1,245	1,008	[1] 816	839	[1] 926	908	675	368	478	806
V	265	409	[1] 352	203	[1] 241	371	80	274	198	[1] 160	255
Total	1,390	2,149	1,905	1,370	1,397	1,509	1,212	1,201	772	878	1,378
Portage Entry:											
III	[1] 280	147	202	208	392	594	231	340	209	146	275
IV	290	607	549	533	637	502	534	547	265	301	477
V	247	226	33	38	393	55	137	243	155	[1] 94	162
Total	817	980	784	779	1,422	1,151	902	1,130	629	541	914
Marquette:											
III	[1] 199	142	143	201	250	83	124	128	135	139	154
IV	406	430	517	344	246	242	210	259	229	191	308
V	143	230	54	88	204	103	44	45	86	[1] 84	108
Total	748	802	714	633	700	428	378	432	450	414	570

[1] Estimated by procedure explained in text.

records for the year classes in the Portage Entry samples illustrate this variability. The strongest year class (1950) and the third strongest (1953) held their ranks by reason of catches well above the 10-year average (given in right-hand column of table 11) at all three ages; similarly, the weakest year class (1955) yielded catches well below average as the III group and the IV group (V group estimated), and the next to the weakest (1954) was taken in below-average numbers at all three ages (though near average as age group V). The next to strongest year class (1951), on the contrary, held that position because of tremendous numbers caught as age group III (over twice the mean of 275); its representation was only moderately above average as age group IV and was extremely low as age group V. The 1947 year class held a rank above average only because of a strong upward trend of the catches; the numbers were far below average as age group III, above average as age group IV, and highest (relatively) as age group V. The catches of the remaining year classes from Portage Entry can be described best as variable but without clear trend. Two examples should illustrate the situation. The 1947 year class was weakly represented as age group III, but catches as age groups IV and V were sufficient to bring the total above average. In the 1952 year class, the poor catches as age groups III and V were counterbalanced by the good catch as age group IV to bring the total near the mean.

Numerous causes can be advanced for the discrepancies among successive samples of certain year classes, but no clear demonstration or evaluation can be offered for any of them. Random error unquestionably played a role because none of the annual samples was truly large and some were undesirably small (table 1). Major sources of bias were weather, nature of previous fishing on the year class, and changes of gear specifications.

The shortness of the spawning season in late November and early December makes the success of fishing highly sensitive to weather. Near the height of spawning, a storm that is severe enough to damage gear and disperse the schools depresses the catch per unit effort and causes underestimates of the strength of year classes represented in the year's sample. Conversely, exceptionally calm, favorable weather can make the catch per unit effort higher than normal. Should the weather, by mischance, cause the catch per unit effort to be abnormally high or low in 2 or all of the 3 years in which a year class is present in numbers, a severe misjudgment must result. It was not possible to relate weather conditions to the behavior of estimates of year-class strength at successive ages. Storms cannot be classified satisfactorily as to the expected effect on catch per unit effort, and furthermore the effects of a single storm are not uniform for all gear in an area. It is only to be hoped that biases from weather conditions were not cumulative for many year classes and that for most they were compensatory.

Intensity of fishing or fishing conditions that influence the vulnerability of a year class in its first year or years of exploitation can influence later estimates of its strength. If, for example, a year class is highly vulnerable to the nets and fished heavily as age group III, the original numbers may be so reduced that catches as age groups IV and V are relatively low. If both age groups III and IV are removed in large numbers, the return per unit effort as the V group may be extremely small. Low vulnerability and low removal at the earlier ages should have the reverse influence. Effects of earlier fishing against year classes may well have contributed to the discrepancies among age groups and to the upward or downward trends described for the Portage Entry samples and present in those from the other two ports.

As was pointed out in the section on materials and methods, many fishermen increased the mesh size of lake herring gill nets during the years of sampling. A second change of gear was the gradual conversion from cotton to nylon twine. The change of mesh size was an adjustment to the increase in the mean size of the lake herring and tended to maintain the capacity of the gear to take fish in constant relation to the true abundance of lake herring on the grounds. Fishermen who did not increase mesh size as fish size increased probably lowered the relative efficiency of their nets. The conversion from cotton to nylon almost certainly increased the catching power of the nets. It is not possible, however, to offer quantitative estimates of the effects of either the increases of mesh size or the change in netting material.

Other possible sources of bias to the samples could be stated but the chance that any of them were significant is too small to justify even a listing.

Even though the discrepancies that appear in the data for certain year classes at each port can be explained logically, the explanations do not weaken the necessary conclusion that certain of the estimates of year-class strength are less precise than might be wished. The method which appears least biased for judging the strength of each year class is one based on the number of fish caught per unit of effort for the three age groups combined.

The apparent strength of the year classes (see year-class totals of table 11) varied considerably but not excessively at each port. The richest year class at Bayfield (1947—2,149 fish at three ages) was 2.78 times as strong as the weakest (1954—772 fish). The strongest year class at Portage Entry (1950) yielded catches that were 2.63 times those of the weakest (1955), and at Marquette the catches of the 1947 year class were 2.12 times those of the 1952 year class. These 2.12- to 2.78-fold fluctuations may appear substantial but they are trivial in comparison with the 88.5-fold fluctuation of year-class strength determined by Pycha (1961) for the Green Bay walleye.

The year-to-year fluctuations of year-class strength at each port are grasped best from the data of table 12 (see also fig. 4) in which each year-class total of table 11 is expressed as a percentage deviation from the mean for the 10 year classes. It is obvious at once that fluctuations at Bayfield and Marquette had many

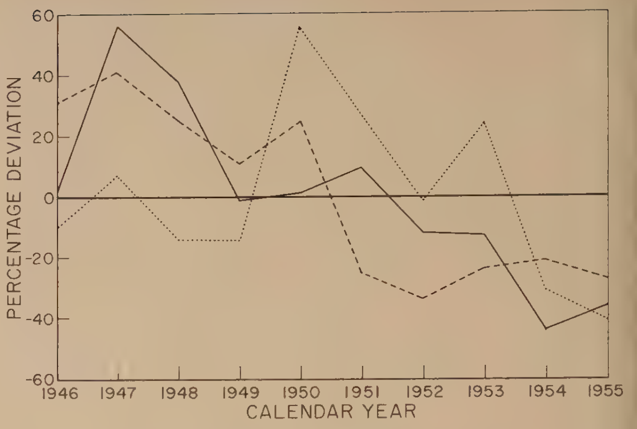

FIGURE 4.—Fluctuations in the relative strength of the year-classes 1946–55 of lake herring from Bayfield (solid line); Portage Entry (dotted line); and Marquette (dashes).

TABLE 12.—*Fluctuations of year-class strength of lake herring off three Lake Superior ports*

[Percentage deviations computed from year-class totals of table 11]

Year class	Percentage deviation from average for port		
	Bayfield	Portage Entry	Marquette
1946	0.8	−10.6	31.3
1947	55.9	7.3	40.7
1948	38.2	−14.2	25.3
1949	−.6	−14.7	11.1
1950	1.4	55.7	22.8
1951	9.5	26.0	−24.9
1952	−12.1	−1.3	−33.7
1953	−12.8	23.7	−24.2
1954	−44.0	−31.1	−21.0
1955	−36.3	−40.8	−27.4

similarities but exhibited only limited agreement with those off Portage Entry.

The deviations from average at Bayfield and Marquette were on the same side of the average for 8 of 10 year classes. Year classes off the two ports agreed particularly well in 1947 (the best year class at each port) and 1948 when year classes were strong and in 1952–55 when all four year classes were decidedly below average. Agreement was poor in 1946, 1949, and 1950 which produced year classes near average at Bayfield and above average at Marquette; the 1951 year class produced the worst disagreement—9.5 percent above average at Bayfield and 24.9 percent below at Marquette.

The closeness of the agreement between year-class fluctuations at Bayfield and Marquette is brought out by the coefficient of correlation ($r=0.726$) between the deviations from average. This value of the coefficient is significant at the 2-percent probability level ($r=0.716$ at $p=0.02$; $df=8$).

The data for Portage Entry agreed clearly with those for Bayfield and Marquette in 1954 and 1955 when the year classes were decidedly weak off all three ports but showed most limited agreement in other years.

Data for Bayfield and Portage Entry agreed in some measure in 1947 and 1951 when year classes were above average at both ports. Year classes of 1946, 1949, 1950, and 1952 were near average at one of the two ports but departed from average by at least 10.6 percent and as much as 55.7 percent at the other. Major disagreements between Bayfield and Portage Entry were provided by the year classes of 1948 and 1953.

The only consequential agreement between records for Portage Entry and Marquette, aside from the previously mentioned 1954 and 1955 year classes, was provided by the year classes of 1947 and 1950. The agreement for 1952 was unimportant, and disagreements were major for the year classes of 1946, 1948, 1949, 1951, and 1953.

No attempt has been made yet to inquire into the factors of year-class fluctuation in Lake Superior stocks of lake herring or into the reasons for the broad similarities of these fluctuations at Bayfield and Marquette and the apparently independent fluctuations at Portage Entry. A longer series of data is needed.

SIZE AT CAPTURE

LENGTH AND WEIGHT OF THE AGE GROUPS

Data on length and weight of the age groups (table 13) provide comparisons by sex, port, and two periods of capture (1950–55 and 1956–59). The females were longer than the males in 20 of 24 comparisons at Duluth, Bayfield, and Portage Entry, and the males held an advantage (7 of 10 comparisons) at Marquette. Among the best represented age groups (III–V), sex differences in average length were small. The largest advantage for the females was 0.6 inch (V groups in the Duluth collections); the largest for the males was 0.2 inch at Marquette (III group in the 1950–55 and the IV group in the 1956–59 samples)

Table 13.—*Average total lengths and weights of the age groups of male and female lake herring according to port and period of capture*

Age group and sex	Duluth		Bayfield				Portage Entry				Marquette			
	1957–59		1950–54		1956–59		1950–55		1956–59		1950–55		1956–59	
	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight
	Inches	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*
I:														
Males	11.3	6.3			11.7	7.0	11.3	6.3	11.9	7.4	11.7	7.0	12.6	8.8
Females					11.8	7.2	11.5	6.7	12.0	7.6	11.3	6.3	12.3	8.2
II:														
Males	11.3	6.3	11.0	5.8	11.8	7.2	11.4	6.5	12.0	7.6	11.7	7.0	12.7	9.0
Females	11.9	7.4	11.3	6.3	11.9	7.4	11.5	6.7	12.0	7.6	11.9	7.4	12.7	9.0
V:														
Males	11.9	7.4	11.1	6.0	11.8	7.2	11.4	6.5	12.1	7.8	11.9	7.4	12.9	9.6
Females	12.1	7.8	11.5	6.7	12.2	8.0	11.8	7.2	12.3	8.2	12.0	7.6	12.7	9.0
:														
Males	11.6	6.8	11.5	6.7	11.9	7.4	11.5	6.7	12.6	8.8	12.2	8.0	12.9	9.6
Females	12.2	8.0	11.8	7.2	12.4	8.4	11.8	7.2	12.7	9.0	12.1	7.8	12.8	9.3
I:														
Males	12.3	8.2	12.8	9.3	12.8	9.3	11.1	6.0	11.6	6.8	12.8	9.3	14.0	12.3
Females	12.8	9.3	12.5	8.6	12.7	9.0	11.6	6.8	12.8	9.3	11.7	7.0	13.2	10.3
II:														
Males	15.6	17.2												
Females	12.4	8.4			12.8	9.3								

It is difficult, if not impossible, to distinguish possible true sex differences in the growth of Lake Superior lake herring from the effect of bias from segregation by size and maturity and the resulting selective action of the fishery on the population. Since male lake herring mature at a slightly younger age than do females, a substantially larger percentage of males than females were represented in age groups II and III at all ports except Marquette (table 9). The intensive lake herring fishery at the ports west of Marquette selectively destroyed these early-maturing, fast-growing males in the younger age groups, leaving the slower growing, late-maturing members of the sex to represent the older age groups. This phenomenon may well lead to low estimates of size for males in the older age groups. Since the lake herring from Marquette grew faster than those from the other ports, proportionately larger numbers of mature females were represented in the younger age groups. The sex ratio, therefore, was more nearly equal in age groups II and III and the fishery which has never been intensive at Marquette, was not particularly selective toward the males.

A detailed discussion of table 13 is not desirable as more discriminating information is given in the section on calculated growth. Most of the lake herring, regardless of age, fell within the 11- to 13-inch range and weighed 6 to 10 ounces. The small difference in size among the age groups is surely a result of the highly selective gill nets, segregation by maturity, and of selective fishing mortality.

With only one exception (that of the VI-group males in the 1956–59 Bayfield collections), the average size of the age groups was larger in 1956–59 than in 1950–55. Among the best represented age groups (III–V), the increase in length from the early to the late period ranged from 0.4 inch to 1.1 inches (11.5 to 11.9 inches for the V-group males at Bayfield and 11.5 to 12.6 inches for the V-group males at Portage Entry). In general, the average size of the lake herring increased from the western to the eastern part of the lake. Lake herring of age groups III–V from the 1956–59 Marquette collections were 0.6 so 1.4 inches longer and 1.3 to 2.7 ounces heavier than fish of the same age from Duluth.

LENGTH DISTRIBUTION OF THE SAMPLES

The length-frequency records for the samples (table 14), by port and period of capture, indicate generally compact distributions. The range in length from the shortest to the longest fish was greatest (6.9 inches) in the Duluth samples and smallest (3.9 inches) in the 1950–55 Portage Entry collections. The Duluth samples were represented by both the shortest (9.0 inches) and the longest (15.9 inches) fish taken in all of the collections.

TABLE 14.—*Length distribution of Lake Superior lake herring according to port for the periods 1950–55 and 1956–59*

[Asterisks indicate modes]

Total length	Duluth	Bayfield		Portage Entry		Marquette	
	1957–59	1950–54[1]	1956–59	1950–55	1956–59	1950–55	1956–59
Inches							
9.0–9.4	1	--------	--------	--------	--------	--------	--------
9.5–9.9	4	3	--------	--------	--------	--------	--------
10.0–10.4	12	21	1	5	1	1	--------
10.5–10.9	13	106	18	61	13	2	5
11.0–11.4	43	*198	58	180	60	15	11
11.5–11.9	61	130	155	*235	183	91	46
12.0–12.4	*114	53	*167	102	*201	143	116
12.5–12.9	55	17	89	11	139	*195	*148
13.0–13.4	19	6	21	2	66	91	141
13.5–13.9	1	1	6	1	24	13	71
14.0–14.4	1	--------	1	--------	7	3	12
14.5–14.9	--------	--------	--------	--------	--------	2	2
15.0–15.4	--------	--------	--------	--------	--------	--------	--------
15.5–15.9	1	--------	--------	--------	1	--------	2
Number of fish	325	535	516	597	695	556	554
Average length	11.9	11.3	12.0	11.6	12.2	11.9	12.8
Percentage over 11.9 inches	58.8	14.4	55.0	19.4	63.0	80.4	88.8

[1] Samples were not collected in 1953 and 1955.

The length composition clearly changed from 1950–55 to 1956–59 at two of the three ports. From the earlier to the later period, the modal length increased 1.0 inch at Bayfield (from 11.0–11.4 to 12.0–12.4 inches) and 0.5 inch at Portage Entry (11.5–11.9 to 12.0–12.4 inches). The mean length increased 0.7 inch (from 11.3 to 12.0 inches) at Bayfield and 0.6 inch (11.6 to 12.2 inches) at Portage Entry. The mode at Marquette (12.5–12.9 inches) was the same for the two periods but the mean length increased 0.7 inch (11.9 to 12.8 inches). Port-to-port differences of modal length were greatest in the 1950–55 samples; the mode was 11.0–11.4 inches at Bayfield, 11.5–11.9 inches at Portage Entry, and 12.5–12.9 inches at Marquette. The average lengths increased from 11.3 inches at Bayfield to 11.6 at Portage Entry and 11.9 at Marquette.

The percentage of fish longer than 11.9 inches varied with differences in modal and mean lengths. The percentage of lake herring 12.0 inches long or longer in the 1950–55 collections was 14.4 at Bayfield, 19.4 at Portage Entry, and 80.4 at

Marquette. The percentages were higher in 1956–59 at all ports—58.5 percent at Duluth (no earlier data), 55.0 percent at Bayfield, 63.0 percent at Portage Entry, and 88.8 percent at Marquette.

LENGTH DISTRIBUTION OF THE AGE GROUPS

The records on the length-frequency distributions of the age groups have been limited to one example, that of the 1957 Marquette collection (table 15). It is not believed that the additional information to be gained would warrant the large expansion of tabular material to show the length distributions of the age groups for each year or period at each port. The 1957 Marquette sample was selected because it illustrates the general characteristics of all the samples.

Table 15.—*Length distribution of the age groups of Lake Superior lake herring captured at Marquette, 1957*

Total length	Age group				
	II	III	IV	V	VI
Inches					
11.0–11.4			1	1	
11.5–11.9	1	3	7		
12.0–12.4	1	14	16	5	1
12.5–12.9	3	16	24	3	
13.0–13.4	2	9	31	4	1
13.5–13.9		4	8	2	
14.0–14.4			1		
14.5–14.9					
15.0–15.4					
15.5–15.9					1
Total	7	46	88	15	3
Average length	12.6	12.7	12.8	12.7	13.6

Typical of the length distributions of the age groups of Lake Superior lake herring are the small ranges of length and the extensive overlap of the age groups. The range in length of the age groups of the 1957 Marquette sample was only 1.9 inches for age group II to 3.9 inches for the VI-group fish. Despite the small range, over-ap was extensive. The length interval of 12.0–13.4 inches was represented by all five age groups.

LENGTH-WEIGHT RELATION

GENERAL RELATION

The data on general length-weight relation of the Lake Superior lake herring (table 16) were based on fish from all of the collections regardless of port, year, or season of capture, type of gear, sex, or state of maturity. The length-weight relation does vary according to port and year of capture, and between ripe and fully spent females, but it was held that the best estimate of the general relation is one based on all available fish. The empirical weights at different lengths are given graphically by dots in figure 5. The curve is a graph of the following equation derived by fitting a straight line (by least squares) to the logarithms of the average lengths and weights:

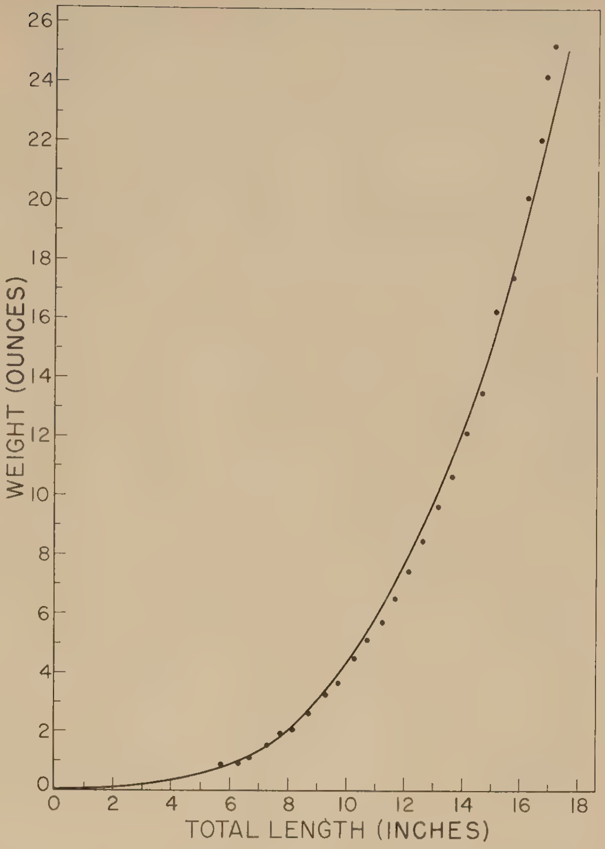

Figure 5.—Length-weight relation of Lake Superior lake herring. The curve represents the calculated weights and the dots the empirical weights.

$$\text{Log } W = -2.54688 + 3.17008 \log L,$$

where W=weight in ounces
and L=total length in inches.

Although the calculated weights were higher than the empirical weights for fish between 9.2 and 15.2 inches long, the agreement between the empirical and calculated values was acceptable. The largest disagreement was at 17.55 inches where the empirical weight (28.50 ounces) was 3.52 ounces above the calculated weight (24.98 ounces); only 2 fish were weighed, however, at

Table 16.—*Length-weight relation of Lake Superior lake herring of the combined collections, 1950–59*

Number of fish	Total length	Weight	
		Empirical	Calculated
	Inches	*Ounces*	*Ounces*
12	5.73	0.83	0.72
20	6.27	.97	.96
11	6.63	1.14	1.14
13	7.24	1.53	1.51
24	7.72	1.86	1.85
20	8.18	2.13	2.22
25	8.70	2.69	2.70
25	9.22	3.26	3.25
29	9.70	3.66	3.81
72	10.28	4.54	4.58
444	10.76	5.11	5.30
1,216	11.23	5.76	6.07
1,896	11.68	6.51	6.87
2,068	12.19	7.42	7.87
1,314	12.68	8.41	8.92
682	13.17	9.66	10.05
284	13.65	10.68	11.26
118	14.17	12.18	12.68
101	14.67	13.56	14.15
72	15.20	16.22	15.84
47	15.66	17.51	17.41
35	16.22	20.74	19.46
23	16.66	22.15	21.18
11	17.18	25.26	23.35
2	17.55	28.50	24.98

this interval. Most disagreements were less than 0.5 ounce.

INCREASE OF WEIGHT FROM 1950–55 TO 1956–61

The annual data on the length-weight relation of Lake Superior lake herring have been combined for 1950–55 and 1956–61. This arbitrary division seems to be best for showing the long-term changes in weight for the 12-year period. Year-to-year differences in 1950–55 were without trend at each of the ports, but weights of fish of the same length showed a definite upward trend from 1956 through 1961. The data of table 17 are based entirely on records of weights of spawning-run male lake herring. Although the weights of the females exhibited trends similar to those of the males, these trends were often obscured by sample differences in the proportions of ripe, partially spent, or spent fish. Weight differences between fully ripe and spent females are considered too severe for the data to be included in this study. Deason and Hile (1947), for example, demonstrated that the loss of weight of the female *C. kiyi* at spawning amounted to 11.8 percent, whereas the loss of weight of males was altogether unimportant (mean percentage loss, 1.6).

The differences of weight in the two collecting periods were strongly consistent. Among comparisons of length intervals represented by 10 or more fish in each period, lake herring captured in 1956–61 were without exception heavier than those of the same length taken in 1950–55 (table 17).

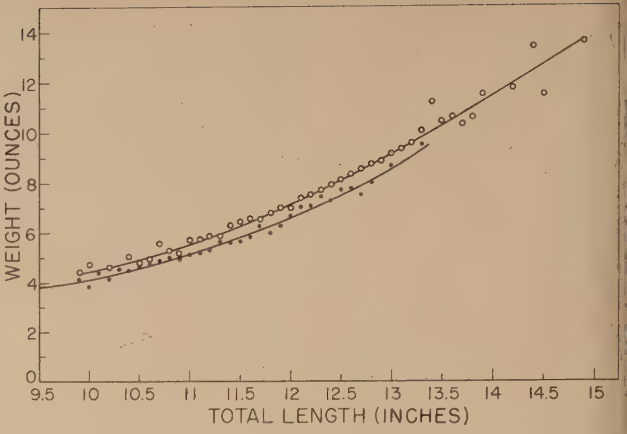

Figure 6.—Weights of Bayfield lake herring captured in 1950–54 (solid dots) and in 1956–61 (open dots). The curves were fitted by inspection.

The percentage increase in weight, length for length, ranged from 4.1 to 13.4 at Bayfield (fig. 6). The percentage increases in weight at the other ports ranged from 2.3 to 6.9 at Portage Entry and from 2.7 to 9.7 at Marquette. The average percentage increase in weight was greatest at Bayfield (8.8 percent), followed by Marquette (5.2 percent), and Portage Entry (4.4 percent). When the numbers of fish were small, lake herring caught in 1950–55 occasionally were heavier than those of the same length taken in 1956–61, but even here the 1956–61 fish were heavier in the great majority of the comparisons.

Despite the fact that mesh sizes of the commercial gill nets were frequently larger in 1956–61 than in 1950–55, lake herring of the same length were heavier during the later period regardless of the mesh size of the net from which they were taken.

Port-to-port differences in average weights among fish of the same length in 1950–55 showed a west-to-east trend toward increased weight. Comparisons of weights for length intervals represented by 5 or more fish from each port revealed the Marquette lake herring to be the heaviest in 9 of 14 comparisons, fish from Portage Entry ranked second in 9 of 14 comparisons, and the Bayfield lake herring were lightest in 13 of 14 comparisons. In 1956–61, the Marquette lake herring were heaviest in 7 of 11 comparisons, but port-to-port differences in weight among fish from Duluth, Bayfield, and Portage Entry were small and without trend.

TABLE 17.—*Weights of spawning-run male lake herring taken in Lake Superior during 1950–55 and 1956–61*

Total length	Duluth		Bayfield				Portage Entry				Marquette			
	1956–60[1]		1950–54[2]		1956–61		1950–55		1956–61		1950–54[3]		1956–61	
	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight
Inches		*Ounces*		*Ounces*		*Ounces*		*Ounces*		*Ounces*		*Ounces*		*Ounces*
5	1	3.80	1	3.90	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------
6	1	3.90	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------
7	2	4.25	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------
8	--------	--------	--------	--------	--------	--------	1	4.0	--------	--------	1	3.89	--------	--------
9	1	4.50	4	4.15	1	4.40	--------	--------	--------	--------	--------	--------	--------	--------
.0	--------	--------	1	3.84	1	4.70	--------	--------	--------	--------	1	4.08	--------	--------
.1	3	4.27	3	4.41	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------
.2	2	4.35	7	4.19	1	4.60	2	4.53	1	4.70	--------	--------	--------	--------
.3	2	4.70	4	4.52	--------	--------	1	4.30	--------	--------	1	4.36	--------	--------
.4	7	4.66	11	4.49	2	5.00	4	4.77	--------	--------	--------	--------	--------	--------
.5	--------	--------	16	4.70	2	4.75	4	4.79	--------	--------	13	4.78	--------	--------
.6	3	5.23	21	4.78	3	4.93	7	4.89	--------	--------	1	4.87	--------	--------
.7	2	5.25	34	4.85	4	5.58	16	5.05	3	4.87	8	5.31	1	5.30
.8	7	5.14	49	4.95	6	5.28	18	5.19	3	5.37	9	5.13	1	5.90
.9	4	5.38	45	4.97	5	5.16	23	5.26	3	5.27	4	5.62	1	5.50
.0	7	5.36	48	5.17	8	5.64	32	5.32	8	5.54	11	5.23	1	5.20
.1	8	5.85	38	5.21	5	5.72	35	5.48	7	5.60	18	5.69	1	6.30
.2	10	5.70	48	5.36	19	5.81	41	5.66	11	6.05	31	5.76	--------	--------
.3	6	6.20	38	5.61	24	5.84	57	5.78	9	5.73	44	5.81	3	6.63
.4	9	6.14	21	5.64	19	6.22	50	5.91	9	6.11	61	6.02	3	6.63
.5	13	6.29	23	5.66	23	6.40	55	6.14	5	6.24	77	6.14	--------	--------
.6	12	6.41	15	5.89	34	6.51	53	6.18	21	6.47	65	6.13	4	6.42
.7	8	6.75	10	6.26	22	6.56	54	6.36	28	6.68	80	6.37	5	7.06
.8	10	6.87	10	5.99	39	6.79	33	6.46	24	6.71	100	6.48	7	8.02
.9	15	7.09	4	6.28	29	6.93	38	6.70	19	6.88	90	6.77	4	6.66
2.0	13	7.07	5	6.65	34	6.99	54	6.83	21	6.98	123	6.89	13	7.56
2.1	16	7.17	12	7.00	32	7.38	32	7.04	12	7.23	102	7.07	18	7.70
2.2	12	7.68	2	7.02	29	7.43	33	7.09	14	7.42	92	7.26	18	7.63
2.3	9	7.49	5	7.47	21	7.66	18	7.27	12	7.77	72	7.47	19	7.96
2.4	5	7.82	1	7.23	36	7.93	12	7.47	14	7.76	86	7.59	19	7.94
2.5	10	7.98	1	7.72	24	8.10	8	7.46	11	8.06	69	7.71	22	8.08
2.6	9	8.46	2	7.78	27	8.31	4	7.74	11	8.36	69	8.01	24	8.24
2.7	7	8.67	2	7.53	19	8.53	4	7.99	13	8.12	56	8.24	26	8.46
2.8	4	8.15	1	8.01	18	8.77	3	8.25	8	8.85	33	8.32	28	8.59
2.9	5	8.92	--------	--------	11	8.88	--------	--------	5	8.72	27	8.69	24	9.11
3.0	4	8.80	1	8.61	9	9.14	1	8.25	7	9.14	9	8.95	32	9.06
3.1	3	9.30	--------	--------	14	9.34	--------	--------	6	9.43	14	9.09	28	9.48
3.2	2	8.85	--------	--------	7	9.59	--------	--------	5	9.84	7	9.16	28	9.56
3.3	3	9.27	1	9.52	4	10.08	--------	--------	3	10.13	3	9.71	26	9.69
3.4	1	7.20	--------	--------	1	11.20	--------	--------	5	9.62	4	9.52	24	10.05
3.5	--------	--------	--------	--------	6	10.37	--------	--------	1	10.20	2	10.14	24	10.14
3.6	4	9.65	--------	--------	4	10.58	1	11.57	10	10.25	--------	--------	26	10.06
3.7	--------	--------	--------	--------	2	10.30	--------	--------	3	10.27	1	12.35	11	10.54
3.8	--------	--------	--------	--------	1	10.60	--------	--------	2	10.45	1	10.51	12	10.90
3.9	--------	--------	--------	--------	1	11.50	--------	--------	1	11.50	1	11.61	11	10.87
4.0	--------	--------	--------	--------	--------	--------	--------	--------	2	10.75	--------	--------	9	10.67
4.1	--------	--------	--------	--------	--------	--------	--------	--------	3	11.10	1	9.88	3	11.23
4.2	--------	--------	--------	--------	1	11.80	--------	--------	--------	--------	--------	--------	4	12.12
4.3	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	1	12.70	3	11.60
4.4	--------	--------	--------	--------	1	13.40	--------	--------	1	12.80	--------	--------	3	12.53
4.5	--------	--------	--------	--------	1	11.50	--------	--------	1	11.30	--------	--------	3	11.67
4.6	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	1	13.10
4.7	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	3	12.67
4.8	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	1	14.50
4.9	--------	--------	--------	--------	2	13.60	--------	--------	--------	--------	1	16.58	--------	--------
5.5	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	1	17.99
5.8	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	1	17.81	1	16.40

[1] Samples were not collected in 1961. [2] Samples were not collected in 1953 and 1955. [3] Appropriate samples were not available for 1955.

CALCULATED GROWTH

GROWTH IN LENGTH

The growth rate of the Lake Superior lake erring varied considerably but in general tended o be faster in the later collections. A division in he data accordingly was made to separate a eriod of relatively slow growth (1950–55) from period of more rapid growth (1956–59). A deailed discussion of annual fluctuations in growth s presented in a later section.

The calculated lengths of the sexes (data not given here) revealed slightly higher values for the females at Duluth, Bayfield, and Portage Entry, and greater lengths for the males at Marquette. The differences were small, never exceeding 0.6 inch. True sex differences in growth rate have been observed in only one stock of lake herring, that of Clear Lake in northeastern Wisconsin, where Hile (1936) demonstrated that the calculated lengths of the females were up to 0.3 inch longer than those of the males.

TABLE 18.—*Calculated total length of lake herring taken at Duluth in 1957–59*

Age group	Number of fish	Calculated length at end of year of life							
		1	2	3	4	5	6	7	8
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	9	4.8	8.5	[1] 11.3					
III	76	4.8	7.4	9.9	[1] 11.5				
IV	142	4.2	6.8	8.9	10.7	[1] 12.0			
V	78	3.9	6.3	8.1	9.8	11.1	[1] 12.0		
VI	18	4.1	6.5	8.2	9.7	10.9	11.9	[1] 12.7	
VII	2	3.9	6.6	8.3	9.6	10.8	12.3	13.3	[1] 14.0
Grand average [2]		4.3	6.8	9.0	10.6	11.6	12.5	13.3	14.0
Number of fish		325	325	325	316	240	98	20	2

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

Since it appears impossible to distinguish true sex differences in growth of Lake Superior lake herring from the effect of bias through the selective action of the fishery on a population segregated by maturity, the sexes have been combined for the study of calculated growth.

The major difficulties in the estimation of growth of Lake Superior lake herring arise from the systematic decline in calculated growth rate with an increase in age. These discrepancies were similar in the data for all of the collections at each port (tables 18 through 24). The situation is described best by a few examples. First-year calculated lengths of lake herring from Duluth decreased from 4.8 inches for the II group to 3.9 inches for age group V (table 18); at Bayfield, the decrease was from 5.6 inches for the II group to 4.3 inches for the VI group in the 1956–59 collections (table 20). Second-year calculated lengths decreased from 9.6 inches (II group) to 5.7 inches (VI group) in the 1956–59 Portage Entry samples (table 22) and from 9.8 inches for age group II to 6.5 inches for age-group VI in the 1956–59 Marquette collections (table 24). A detailed review of the comments of other investigators on this kind of disagreement is not considered necessary here since systematic discrepancies of this type have been observed repeatedly among the lake herring and other species and have been discussed at length in the literature. Most investigators agree that the high calculated lengths of the younger age groups and the low values for the older fish can be traced to two major sources of bias: gear selection of the larger fish in the younger age groups and the progressive destruction of the faster growing fish by the fishery. These sources of bias, combined with segregation by maturity of the spawning-run samples, undoubtedly account for the discrepancies among the calculated growth histories of Lake Superior lake herring.

TABLE 19.—*Calculated total length of lake herring taken at Bayfield in 1950–54* [1]

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
III	129	4.8	7.6	9.4	[2] 11.2			
IV	328	4.5	7.0	8.7	10.4	[2] 11.3		
V	74	4.4	6.7	8.4	9.8	11.0	[2] 11.7	
VI	5	4.5	6.7	8.4	9.7	10.8	11.8	[2] 12.6
Grand average [3]		4.6	7.1	8.8	10.5	11.2	11.9	12.7
Number of fish		536	536	536	536	407	79	5

[1] Samples were not collected in 1953.
[2] Average length at capture following completion of current-season growth.
[3] Based on the successive addition of mean increments beyond the fifth year of life.

The two major sources of bias to estimates of growth are to some degree compensating. The best estimates of general growth are held, therefore, to be those based on records from all the fish from each of the spawning-run collections. Fish collected by the *Siscowet* and from the summer commercial fishery have been omitted from the study to permit comparisons among the spawning-run collections at the various ports.

The extent of the variation of growth of Lake Superior lake herring according to port and period of capture is seen best from the summary in table 25. The fish from Bayfield were the slowest growing in the 1950–55 samples, and those from Marquette had the fastest growth (fig. 7). Portage Entry lake herring grew faster than the Bayfield fish but more slowly than those from Marquette. First-year calculated lengths ranged from

TABLE 20.—*Calculated total length of lake herring taken at Bayfield in 1956–59*

Age group	Number of fish	Calculated length at end of year of life							
		1	2	3	4	5	6	7	8
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	17	5.6	9.3	[1] 11.7					
III	96	4.9	7.8	10.2	[1] 11.8				
IV	296	4.7	7.4	9.2	10.9	[1] 12.0			
V	97	4.6	6.9	8.6	10.1	11.3	[1] 12.2		
VI	6	4.3	6.6	8.4	9.8	11.0	11.8	[1] 12.7	
VII	2	4.8	6.4	7.8	9.0	10.2	11.3	12.3	[1] 12.8
Grand average [2]		4.7	7.4	9.4	10.9	11.8	12.7	13.6	14.1
Number of fish		514	514	514	497	401	105	8	(2)

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

TABLE 21.—*Calculated total length of lake herring taken at Portage Entry, 1950–55*

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	9	5.6	8.7	[1] 11.4				
III	167	5.0	7.6	9.8	[1] 11.4			
IV	322	4.8	7.2	9.0	10.6	[1] 11.6		
V	94	4.6	6.7	8.3	9.9	10.9	[1] 11.7	
VI	5	4.3	5.7	6.9	8.3	9.8	10.7	[1] 11.4
Grand average [2]		4.8	7.2	9.1	10.7	11.4	12.2	12.9
Number of fish		597	597	597	588	421	99	5

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

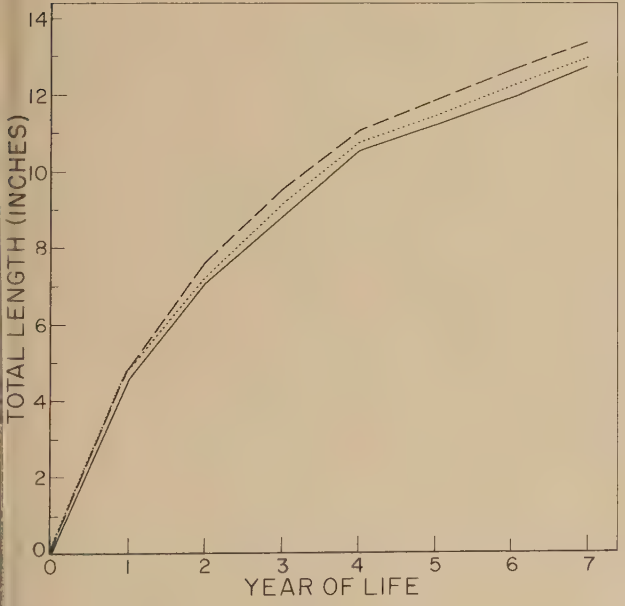

FIGURE 7.—General growth of Lake Superior lake herring of the 1950–55 collections from Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

TABLE 22.—*Calculated total length of lake herring taken at Portage Entry, 1956–59*

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	16	5.6	9.6	[1] 11.9				
III	178	4.9	7.9	10.2	[1] 12.0			
IV	375	4.6	7.2	9.1	11.0	[1] 12.2		
V	123	4.6	6.8	8.6	10.4	11.7	[1] 12.7	
VI	3	3.5	5.7	7.2	8.9	10.6	11.8	[1] 12.2
Grand average [2]		4.7	7.4	9.4	11.1	12.1	13.1	13.5
Number of fish		695	695	695	679	501	126	3

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

TABLE 23.—*Calculated total length of lake herring taken at Marquette 1950–55*

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	5	5.5	9.6	[1] 11.6				
III	129	5.1	8.0	10.2	[1] 11.8			
IV	302	4.7	7.5	9.4	10.9	[1] 11.9		
V	115	4.5	7.2	8.8	10.3	11.4	[1] 12.2	
VI	5	4.4	6.8	8.5	9.9	10.9	11.9	[1] 12.6
Grand average [2]		4.8	7.6	9.5	11.0	11.8	12.6	13.3
Number of fish		556	556	556	551	422	120	5

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

4.6 inches at Bayfield to 4.8 inches at Portage Entry and Marquette. At the end of 4 years of life the calculated lengths were 10.5 inches at Bayfield, 10.7 inches at Portage Entry, and 11.0 inches at Marquette. Sixth-year calculated lengths were 11.9 inches at Bayfield, 12.2 inches at Portage Entry, and 12.6 inches at Marquette.

TABLE 24.—*Calculated total length of lake herring taken at Marquette, 1956–59*

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	22	5.3	9.8	[1] 12.5	-------	-------	-------	-------
III	167	5.5	8.6	10.9	[1] 12.7	-------	-------	-------
IV	271	4.8	7.6	9.7	11.5	[1] 12.8	-------	-------
V	85	4.6	7.2	8.9	10.6	11.8	[1] 12.8	-------
VI	9	4.5	6.5	8.1	9.9	11.2	12.3	[1] 13.4
Grand average [2]	-------	5.0	7.9	10.0	11.7	12.5	13.5	14.6
Number of fish	-------	554	554	554	532	365	94	9

[1] Average length at capture following completion of current-season growth.

[2] Based on the successive addition of mean increments beyond the fifth year of life.

TABLE 25.—*Calculated total length [1] of Lake Superior lake herring according to port for the years 1950–55 and 1956–59*

Year of life	Duluth	Bayfield		Portage Entry		Marquette	
	1957–59	1950–54 [2]	1956–59	1950–55	1956–59	1950–55	1956–59
	Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
1	4.3	4.6	4.7	4.8	4.7	4.8	5.0
2	6.8	7.1	7.4	7.2	7.4	7.6	7.9
3	9.0	8.8	9.4	9.1	9.4	9.5	10.0
4	10.6	10.5	10.9	10.7	11.1	11.0	11.7
5	11.6	11.2	11.8	11.4	12.1	11.8	12.5
6	12.5	11.9	12.7	12.2	13.1	12.6	13.5
7	13.3	12.7	13.6	12.9	13.5	13.3	14.6
8	14.0	--------	14.1	--------	--------	--------	--------

[1] Calculated lengths beyond the fifth year of life are based on the successive addition of mean increments.

[2] Samples were not collected in 1953 and 1955.

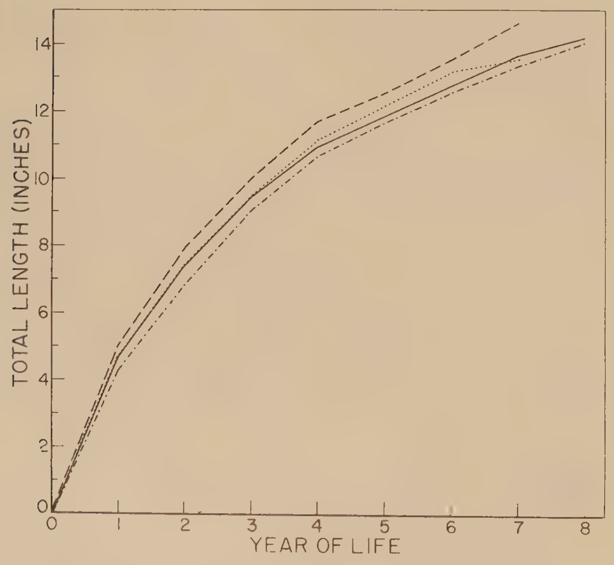

FIGURE 8.—General growth in length of Lake Superior lake herring of the 1956–59 collections from Duluth (dots and dashes), Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

Growth in 1956–59 also increased from the western to eastern ports (fig. 8). The lake herring from Duluth grew 4.3 inches in the first year, those from Bayfield and Portage Entry grew 4.7 inches, and the Marquette fish grew 5.0 inches. In the fourth year of life the calculated lengths of lake herring were 10.6 inches at Duluth, 10.9 inches at Bayfield, 11.1 inches at Portage Entry, and 11.7 inches at Marquette. At the end of 6 years of life the calculated lengths were 12.5 inches at Duluth, 12.7 inches at Bayfield, 13.1 inches at Portage Entry, and 13.5 inches at Marquette.

Dryer (1963) found a similar west-to-east change in the growth of whitefish of Lake Superior. The slowest growing stocks were those from Bayfield; the growth rate increased to the east where the fastest growing fish were from Whitefish Bay. Smith (1956) observed that lake herring from northern Green Bay grew less in their first year than did those from southern Green Bay but grew faster than the southern fish in subsequent years. By the end of the fourth year the differences in size had largely disappeared.

With only one exception (that of the first-year calculated length of the Portage Entry fish) the calculated lengths of lake herring taken at all ports in 1956–59 were greater than those of the 1950–55 collections (fig. 9). The fish taken in the later period at Bayfield were 0.1 inch longer in the first year, 0.6 inch longer in the third, and 0.8 inch longer in the sixth year of life. At Portage Entry the first-year calculated length (4.7 inches) of the 1956–59 fish was 0.1 inch less than that of the 1950–55 samples, but beginning in the second year of life the calculated lengths of the fish taken in the later period were without exception the longer (the largest difference was 0.9 inch in the sixth year of life). Lake herring taken in the later period at Marquette ranged from 0.2 inch longer in the first to 1.3 inches longer in the seventh year of life.

GROWTH IN WEIGHT

The weights in table 26 were computed from the general length-weight equation given on page 509 and correspond exactly with the lengths of table 25. Questions relating to the reliability of the calculated lengths apply, therefore, to the calculated weights.

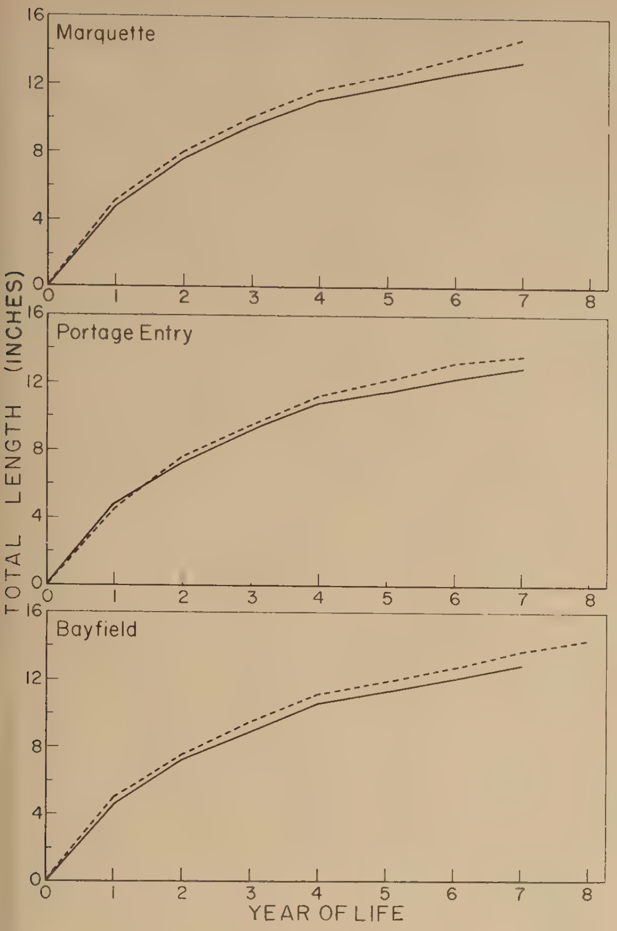

FIGURE 9.—General growth in length of Lake Superior lake herring from Bayfield, Portage Entry, and Marquette. Growth in 1950–55, solid line; in 1956–59, broken line.

TABLE 26.—*Calculated weight of Lake Superior lake herring according to port for the years 1950–55 and 1956–59*

[Weights were computed from the calculated lengths of table 25 by means of the general length-weight equation. Increments in parentheses.]

Year of life	Duluth	Bayfield		Portage Entry		Marquette	
	1957–59	1950–54[1]	1956–59	1950–55	1956–59	1950–55	1956–59
	Ounces	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
	0. 40 (0. 40)	0. 43 (0. 43)	0. 52 (0. 52)	0. 58 (0. 58)	0. 52 (0. 52)	0. 58 (0. 58)	0. 60 (0. 60)
	1. 22 (0. 82)	1. 40 (0. 97)	1. 60 (1. 08)	1. 43 (0. 85)	1. 60 (1. 08)	1. 78 (1. 20)	2. 00 (1. 40)
	3. 04 (1. 82)	2. 82 (1. 42)	3. 58 (1. 98)	3. 18 (1. 75)	3. 58 (1. 98)	3. 64 (1. 86)	4. 33 (2. 33)
	5. 20 (2. 16)	5. 05 (2. 23)	5. 68 (2. 10)	5. 30 (2. 12)	6. 00 (2. 42)	5. 80 (2. 16)	7. 02 (2. 69)
	6. 84 (1. 64)	6. 16 (1. 11)	7. 20 (1. 52)	6. 49 (1. 19)	7. 80 (1. 80)	7. 20 (1. 40)	8. 61 (1. 59)
	8. 61 (1. 77)	7. 40 (1. 24)	9. 10 (1. 90)	8. 00 (1. 51)	10. 10 (2. 30)	8. 84 (1. 64)	11. 10 (2. 49)
	10. 60 (1. 99)	9. 10 (1. 70)	11. 37 (2. 27)	9. 60 (1. 60)	11. 10 (1. 00)	10. 60 (1. 76)	13. 98 (2. 88)
	12. 38 (1. 78)	-------- --------	12. 69 (1. 32)	-------- --------	-------- --------	-------- --------	-------- --------

[1] Samples were not collected in 1953 and 1955.

The calculated weights of lake herring from the various ports differed little at the end of the first year (from 0.4 ounce at Duluth to 0.6 ounce in the 1956–59 Marquette samples), but in subsequent years of life differences among ports and between periods of capture were sometimes considerable.

In 1950–55 the lake herring from Bayfield had the slowest growth in weight (fig. 10). The fish reached 1.4 ounces during the second year of life, and by the seventh year they were 9.1 ounces. Portage Entry fish grew slightly faster than those from Bayfield, reaching 9.6 ounces at the end of 7 years of life. Growth at Marquette was similar to that of fish from the other ports during the first year but was faster in subsequent years; at the end of 7 years the lake herring from Marquette were 1 ounce heavier than those from Portage Entry and 1.5 ounces heavier than the Bayfield fish.

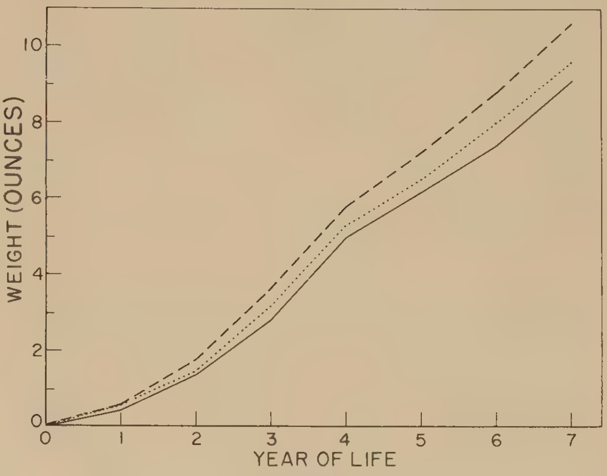

FIGURE 10.—General growth in weight of Lake Superior lake herring in 1950–55 at Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

Growth in weight was faster during 1956–59 than in 1950–55 at all ports. At the end of 6 years of life, for example, the fish from Bayfield were 1.7 ounces heavier in 1956–59 (9.1 ounces) than in 1950–55 (7.4 ounces). At Portage Entry the VI-group fish were 2.1 ounces heavier (increase from 8.0 to 10.1 ounces) and at Marquete they were 2.3 ounces heavier (increase from 8.8 to 11.1 ounces).

Port-to-port differences of growth in weight had a general west-to-east trend toward faster growth during 1956–59 also (fig. 11). Duluth lake herring

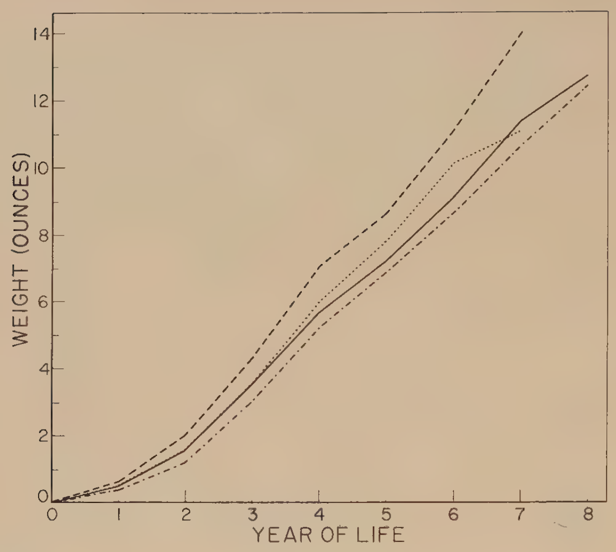

Figure 11.—General growth in weight of Lake Superior lake herring in 1956–59 at Duluth (dots and dashes), Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

weighed 0.4 ounce in the first year, those from Bayfield and Portage Entry grew 0.5 ounce, and at Marquette they grew 0.6 ounce. At the end of 7 years the fish weighed 10.6 ounces at Duluth, 11.4 ounces at Bayfield, 11.1 ounces at Portage Entry, and 14.0 ounces at Marquette.

The second-year increments of weight were more than twice that of the first year's growth at all of the ports except Portage Entry in 1950–55, and third-year growth was double the second-year increments at Duluth and at Portage Entry in 1950–55. The increments in weight reached a peak in the fourth year of life at all ports except Bayfield in 1956–59 and Marquette where the annual increments were highest in the seventh year of life. The largest increment in weight (2.9 ounces) was in the seventh year of life at Marquette in 1956–59.

ANNUAL FLUCTUATIONS IN GROWTH

FLUCTUATIONS OF GROWTH IN LENGTH

Voluminous data and discussions have been published on the extent of annual fluctuations of growth and on the various factors affecting the growth of fish. Temperature and population densities probably have been most commonly considered but the results have been varied and often inconclusive. A discussion of this vast literature need not be undertaken here. Excellent reviews and references to publications on factors of growth have been given by Hile (1936), Van Oosten (1944), and Watt (1956).

The number of studies on factors affecting the growth of lake herring has not been large. Hile (1936), who considered the possible influence of air temperature and population density on the growth of cisco populations in northeastern Wisconsin, concluded that the failure of variations of both factors to operate in the same direction in the same years may obscure the effect of each of them. Van Oosten (1929), Carlander (1945), and Smith (1956) found no correlation between annual fluctuations in growth of lake herring and air temperatures.

The data on annual fluctuations of growth in length of Lake Superior lake herring are separated according to port (tables 27, 28, and 29). Data are given only for age groups III, IV, and V; other groups were not adequately represented. The Duluth samples have been omitted since the collections, available only for 1957–59, cover too few years for a satisfactory study of annual fluctuations.

The growth increments are arranged in the following manner: the columns show the growth for different years of life in a particular calendar year; the horizontal rows show growth in a particular year of life in the different calendar years; and the diagonal rows show the growth history of an age group belonging to a year class that can be identified by the calendar year in which the first-year growth was made. The data for different age groups had to be kept separate because of the systematic discrepancies described in the section on calculated growth in length.

Although examination of the growth increments of lake herring from the various ports reveals strong though irregular trends toward improved growth in the later years, a procedure based on the actual percentage change from one calendar year to the next offers a more precise estimate of growth fluctuations. This method was described in detail by Hile (1941).

The largest annual fluctuations in growth occurred at Bayfield (table 30). Growth was poorest in 1945 and 1946 when the percentage deviations from the 15-year (1945–59) mean were −14.7 and −23.5 percent. Growth improved irregularly to 12.0 percent above average in 1951

TABLE 27.—*Annual increments of growth in length of Lake Superior lake herring captured at Bayfield, 1950–59*

Age groups and years of life	Increment of total length in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
6	-------	-------	-------	-------	-------	0.7	0.7	0.7	-------	0.7	-------	0.7	1.0	1 0	1.2
5	-------	-------	-------	-------	1.6	1.0	1.1	-------	1.4	-------	1.1	1.4	1.2	1.6	-------
4	-------	-------	-------	2.0	1.3	1.6	-------	1.4	-------	1.5	1.8	1.4	1.3	-------	-------
3	-------	-------	1.0	1.3	1.5	-------	1.5	-------	1.6	1.7	1.8	1.5	-------	-------	-------
2	-------	1.3	2.1	2.8	-------	1.3	-------	2.4	2.1	2.3	2.0	-------	-------	-------	-------
1	4.7	4.3	4.6	-------	4.7	-------	4.5	3.9	4.6	4.5	-------	-------	-------	-------	-------
Number of fish	(1)	(19)	(28)	-------	(26)	-------	(22)	(16)	(32)	(27)	-------	-------	-------	-------	-------
Age Group IV:															
5	-------	-------	-------	-------	-------	0.9	1.0	1.0	-------	1.0	-------	1.0	1.1	1.2	1.1
4	-------	-------	-------	-------	1.6	1.5	1.9	-------	1.9	-------	1.9	1.9	1.6	1.9	-------
3	-------	-------	-------	1.7	1.8	1.6	-------	1.9	-------	1.9	1.9	2.2	1.3	-------	-------
2	-------	-------	2.4	2.4	2.6	-------	2.3	-------	2.4	2.5	2.5	3.4	-------	-------	-------
1	-------	4.7	4.4	4.6	-------	4.7	-------	4.7	4.6	4.6	4.7	-------	-------	-------	-------
Number of fish	-------	(63)	(89)	(69)	-------	(107)	-------	(54)	(134)	(43)	(65)	-------	-------	-------	-------
Age group III:															
4	-------	-------	-------	-------	-------	1.7	2.1	1.5	-------	1.4	-------	1.6	1.6	1.3	1.4
3	-------	-------	-------	-------	2.0	1.9	2.5	-------	2.3	-------	2.4	2.4	2.4	2.8	-------
2	-------	-------	-------	2.5	2.6	2.4	-------	2.8	-------	2.7	3.2	2.8	2.9	-------	-------
1	-------	-------	4.9	4.6	5.0	-------	4.9	-------	4.8	4.7	5.4	5.3	-------	-------	-------
Number of fish	-------	-------	(39)	(39)	(24)	-------	(27)	-------	(15)	(41)	(28)	(12)	-------	-------	-------

TABLE 28.—*Annual increments of growth in length of Lake Superior lake herring captured at Portage Entry, 1950–59*

Age groups and years of life	Increment of total length in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
6	-------	-------	-------	-------	-------	0.7	0.7	0.7	1.0	0.9	0.8	0.9	1.0	1.0	1.1
5	-------	-------	-------	-------	1.3	1.0	1.0	1.0	1.0	1.3	1.5	1.3	1.4	1.3	-------
4	-------	-------	-------	1.3	1.5	1.4	1.7	1.8	1.7	1.8	1.7	1.8	1.8	-------	-------
3	-------	-------	1.8	1.6	1.9	1.6	1.9	1.5	1.8	1.8	1.8	1.7	-------	-------	-------
2	-------	2.2	2.2	2.2	1.9	2.0	2.1	2.1	2.2	2.3	2.3	-------	-------	-------	-------
1	4.4	4.5	4.7	4.7	4.3	4.6	4.5	4.3	4.7	4.8	-------	-------	-------	-------	-------
Number of fish	(7)	(28)	(24)	(3)	(3)	(29)	(14)	(31)	(43)	(35)	-------	-------	-------	-------	-------
Age group IV:															
5	-------	-------	-------	-------	-------	1.1	.9	.9	1.1	1.0	.6	1.2	1.3	1.2	1.2
4	-------	-------	-------	-------	1.4	1.6	1.6	1.7	1.6	1.7	1.8	1.9	2.0	1.9	-------
3	-------	-------	-------	1.9	1.9	1.9	1.8	1.9	1.9	1.9	2.0	2.1	2.2	-------	-------
2	-------	-------	2.8	2.5	2.6	2.2	2.1	2.3	2.6	2.6	2.9	2.6	-------	-------	-------
1	-------	4.6	4.6	4.7	4.9	5.2	5.5	4.6	4.5	4.7	4.5	-------	-------	-------	-------
Number of fish	-------	(59)	(69)	(58)	(49)	(50)	(37)	(137)	(123)	(47)	(68)	-------	-------	-------	-------
Age group III:															
4	-------	-------	-------	-------	-------	1.6	1.9	1.7	1.7	1.6	1.8	1.9	1.9	1.5	1.8
3	-------	-------	-------	-------	2.2	2.0	2.2	2.2	2.1	2.1	2.3	2.3	2.3	2.5	-------
2	-------	-------	-------	2.9	2.7	2.5	2.6	2.5	3.0	2.9	3.0	3.9	2.5	-------	-------
1	-------	-------	4.9	4.8	5.0	5.1	5.3	4.9	4.8	5.0	5.0	5.2	-------	-------	-------
Number of fish	-------	-------	(30)	(23)	(22)	(36)	(39)	(17)	(87)	(47)	(26)	(18)	-------	-------	-------

TABLE 29.—*Annual increments of growth in length of Lake Superior lake herring captured at Marquette, 1950–59*

Age groups and years of life	Increment of total length in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
6	-------	-------	-------	-------	-------	1.0	0.7	0.9	0.9	0.9	0.7	0.9	1.1	1.2	1.1
5	-------	-------	-------	-------	0.9	1.1	1.0	1.3	1.3	1.1	1.1	1.3	1.6	1.2	-------
4	-------	-------	-------	1.1	1.5	1.6	1.5	1.6	1.7	1.6	1.8	1.7	1.7	-------	-------
3	-------	-------	2.0	1.4	1.6	1.6	1.7	1.7	1.8	1.6	2.0	1.8	-------	-------	-------
2	-------	2.5	2.9	2.8	2.7	2.7	2.4	2.7	2.6	2.2	2.6	-------	-------	-------	-------
1	4.5	4.5	4.4	4.4	4.4	4.6	4.8	4.4	4.4	4.9	-------	-------	-------	-------	-------
Number of fish	(9)	(21)	(24)	(7)	(21)	(33)	(34)	(15)	(12)	(24)	-------	-------	-------	-------	-------
Age group IV:															
5	-------	-------	-------	-------	-------	1.0	1.1	1.2	1.0	1.0	1.0	1.1	1.3	1.5	1.3
4	-------	-------	-------	-------	1.6	1.4	1.6	1.7	1.8	1.8	1.8	1.8	2.0	1.9	-------
3	-------	-------	-------	1.8	2.0	2.0	2.0	1.9	2.0	2.1	2.1	2.2	2.1	-------	-------
2	-------	-------	2.7	2.8	2.8	2.7	2.7	2.3	2.7	2.8	2.9	2.9	-------	-------	-------
1	-------	4.6	4.7	4.6	4.8	4.8	4.9	4.9	4.9	4.6	4.8	-------	-------	-------	-------
Number of fish	-------	(43)	(63)	(54)	(44)	(59)	(39)	(69)	(88)	(61)	(53)	-------	-------	-------	-------
Age group III:															
4	-------	-------	-------	-------	-------	1.6	1.5	1.5	1.8	1.7	1.6	1.8	1.8	1.9.	1.9
3	-------	-------	-------	-------	2.4	2.0	2.4	2.2	2.1	1.9	2.2	2.5	2.6	2.2	-------
2	-------	-------	-------	2.9	3.4	2.8	2.8	3.1	4.0	4.2	4.1	4.5	3.6	-------	-------
1	-------	-------	4.7	5.0	5.3	5.3	5.5	4.8	5.0	5.0	4.9	5.4	-------	-------	-------
Number of fish	-------	-------	(15)	(21)	(21)	(32)	(20)	(20)	(42)	(46)	(37)	(42)	-------	-------	-------

but then fell to −3.6 percent in 1952. Beginning in 1953, growth improved progressively (exception in 1957) to 1959 when a maximum value of 16.3 percent above average was reached.

Growth at Portage Entry remained below average in 1945–53 (percentage range, from −0.4 to −5.2) and was above average in 1954–59 (exception in 1958). Growth improved steadily from 1952 to 1956 when the value of 8.9 percent above average was reached. The percentage declined in 1957 and 1958 but recovered to 8.7 percent in 1959.

Table 30.—*Percentage deviation of growth in length of Lake Superior lake herring from the 1945–59 mean*

Year	Percentage deviation at			Year	Percentage deviation at		
	Bayfield	Portage Entry	Marquette		Bayfield	Portage Entry	Marquette
1945	−14.7	−4.4	−9.3	1953	−0.9	−0.7	3.1
1946	−23.5	−2.3	−9.3	1954	.1	1.2	1.5
1947	−6.1	−.5	−6.0	1955	6.3	2.5	4.8
1948	−.2	−2.8	−7.9	1956	7.7	8.9	11.2
1949	1.8	−2.5	−1.8	1957	1.0	3.4	11.2
1950	−6.8	−4.1	−.7	1958	10.6	−1.8	6.2
1951	12.0	−.4	−.7	1959	16.3	8.7	−.5
1952	−3.6	−5.2	−1.8				

The percentages of departure from average growth at Marquette fell below the mean in 1945–52 (range, −0.7 to −9.3) and were above average in 1953–58. The maximum value of 11.2 percent occurred in 1956 and 1957, after which the growth rate declined to −0.5 percent in 1959.

With few exceptions, the percentage deviations of growth in length of Lake Superior lake herring at all ports were below average in 1945–53 and above average in 1954–59 (fig. 12). Improvement in growth was especially marked in 1953–56.

To obtain a better measure of the similarity of the long-term changes of growth at the three localities, coefficients of correlation were calculated for the actual annual deviations from average. The coefficients are as follows:

Ports	r
Bayfield–Portage Entry	0.595
Bayfield–Marquette	.618
Portage Entry–Marquette	.601

The coefficients between annual fluctuations in growth were significant at a probability level between 2 and 1 percent (absolute values of r at the 2- and 1-percent levels of significance are 0.592 and 0.641). Conditions as a whole are apparently undergoing a progressive change favorable to improved growth at the three ports. Temperature alone was not responsible for the growth fluctuations of Lake Superior lake herring. Meterological conditions should operate similarly over the entire lake and hence should have similar effects on trends in the growth at all three ports. The temperature records give no evidence, however, for a major upward trend since 1954.

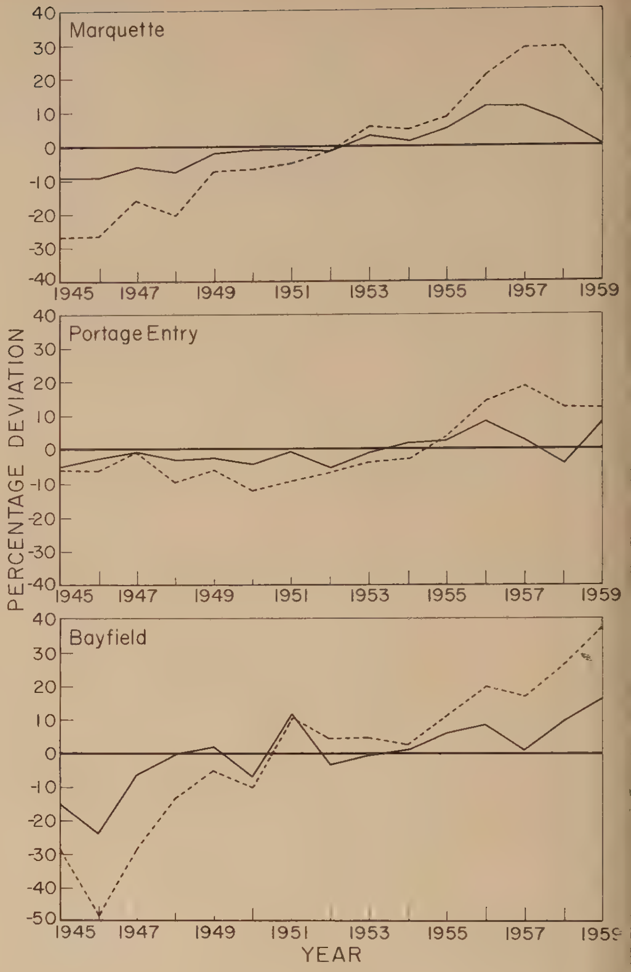

Figure 12.—Annual fluctuations of growth in length (solid line) and weight (broken line), of Lake Superior lake herring from Bayfield, Portage Entry, and Marquette.

The inverse relation which appears to exist between the upward trend in improved growth and the downward trend in abundance of lake herring at the various ports suggests that the decrease in population density may have contributed to the change. A statistically significant correlation between growth (in both length and weight) and abundance could not be established, however. The number of years covered by the data may have been inadequate for a sound statistical analysis. Data on fluctuations of both growth and of abundance in terms of numbers of fish were available only for the 10 years 1950–59. Data on both growth and abundance in terms of pounds of fish were available for 15 years (1945–59) in Michigan waters only.

FLUCTUATIONS OF GROWTH IN WEIGHT

The annual increments of growth in weight (tables 31, 32, and 33) are arranged in the same manner as those of length in tables 27, 28, and 29. Since the calculated weights were based on the calculated lengths, the trends in annual fluctuations of growth in weight for Lake Superior lake herring were similar to those of growth in length (fig. 11). Growth in weight was below average at Bayfield in 1945–50, at Portage Entry in 1945–54, and at Marquette in 1945–52. Growth was above average at all of the ports after 1954.

The correlation between annual fluctuations of growth in weight of Lake Superior lake herring at the three ports was even closer than that for length. The values of *r* follow:

Ports	
Bayfield–Portage Entry	0.651
Bayfield–Marquette	.889
Portage Entry–Marquette	.823

The coefficients were well beyond the 1-percent level of probability, and 2 were beyond the 0.1-percent level.

TABLE 31.—*Annual increments of growth in weight of Lake Superior lake herring captured at Bayfield, 1950–59*

Age groups and years of life	Increment of weight in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
6						1.1	1.0	1.4		1.0		1.2	1.7	1.9	2.2
5					2.2	1.3	1.8		1.9		1.7	2.1	1.8	2.2	
4				1.6	1.2	2.0		1.2		1.8	1.8	1.8	1.3		
3			0.5	.7	1.4		.8		1.2	.9	1.4	1.0			
2		0.4	.7	1.1		.4		.8	.6	.8	.6				
1	0.5	.4	.5		.5		.5	.3	.5	.5					
Number of fish	(1)	(19)	(28)		(26)		(22)	(16)	(32)	(27)					
Age group IV:															
5						1.4	1.5	1.7		1.7		1.7	2.0	2.1	2.1
4					2.1	1.9	2.5		2.6		2.7	2.6	2.3	2.8	
3				1.4	1.4	1.3		1.6		1.6	1.6	2.0	1.4		
2			.9	.8	1.0		.8		.9	.9	.9	1.6			
1		.5	.4	.5		.5		.5	.5	.5	.5				
Number of fish		(63)	(89)	(69)		(107)		(54)	(134)	(43)	(65)				
Age group III:															
4						2.5	3.0	2.2		2.1		2.5	2.6	2.2	2.6
3					1.9	1.8	2.6		2.5		2.5	2.8	3.0	3.6	
2				1.0	.9	1.0		1.2		1.2	1.5	1.5	1.5		
1			.6	.5	.6		.6		.5	.5	.7	.7			
Number of fish			(39)	(39)	(24)		(27)		(15)	(41)	(28)	(12)			

TABLE 32.—*Annual increments of growth in weight of Lake Superior lake herring captured at Portage Entry, 1950–59*

Age groups and years of life	Increment of weight in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
ge group V:	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
6						1.2	1.2	1.3	1.7	1.6	1.5	1.8	1.8	2.2	2.4
5					1.8	1.5	1.5	1.5	1.5	1.9	2.4	2.1	2.4	2.2	
4				1.6	1.7	1.8	2.0	2.1	2.0	2.2	2.0	2.4	2.4		
3			1.2	1.1	1.5	1.0	1.2	1.0	1.2	1.2	1.5	1.4			
2		0.8	.8	.8	.7	.6	.7	.8	.7	.8	.9				
1	0.4	.4	.5	.5	.4	.5	.4	.4	.5	.5					
umber of fish	(7)	(28)	(24)	(3)	(3)	(29)	(14)	(31)	(43)	(35)					
ge group IV:															
5						1.9	1.4	1.5	1.8	1.7	1.2	2.2	2.4	2.6	2.2
4					1.9	2.2	2.2	2.3	2.2	2.5	2.4	2.6	3.1	2.8	
3				1.8	1.6	1.8	1.5	1.8	2.0	1.7	1.8	2.1	2.0		
2			1.1	.9	1.0	.8	.9	1.2	1.0	.9	1.3	.9			
1		.5	.5	.5	.6	.6	.7	.5	.5	.5	.5				
umber of fish		(59)	(69)	(58)	(49)	(50)	(37)	(137)	(123)	(47)	(68)				
ge group III:															
4						2.5	2.8	2.6	2.6	2.4	2.9	3.1	3.2	2.8	3.0
3					2.4	2.0	2.2	2.4	2.3	2.3	2.5	2.7	3.2	2.8	
2				1.3	1.2	1.1	1.2	1.2	1.4	1.3	1.5	2.3	1.2		
1			.6	.5	.6	.6	.7	.6	.5	.6	.6	.6			
umber of fish			(30)	(23)	(22)	(36)	(39)	(17)	(87)	(47)	(26)	(18)			

Table 33.—*Annual increments of growth in weight of Lake Superior lake herring captured at Marquette, 1950–59*

Age groups and years of life	Increment of weight in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1943	1954	1955	1956	1957	1958	1959
Age group V:	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
6	--------	--------	--------	--------	--------	1.8	1.3	1.7	1.7	1.8	1.4	2.0	2.3	2.6	2.6
5	--------	--------	--------	--------	1.3	1.7	1.6	2.1	2.1	1.7	1.9	2.1	2.6	2.2	--------
4	--------	--------	--------	1.5	2.0	2.1	1.9	2.0	2.2	2.3	2.3	2.2	2.4	--------	--------
3	--------	--------	1.7	1.2	1.3	1.3	1.5	1.4	1.7	1.3	1.4	1.7	--------	--------	--------
2	--------	0.8	1.1	1.1	1.0	1.0	.8	1.2	.9	.8	1.1	--------	--------	--------	--------
1	0.5	.5	.4	.4	.4	.5	.5	.4	.4	.6	--------	--------	--------	--------	--------
Number of fish	(9)	(21)	(24)	(7)	(21)	(33)	(34)	(15)	(12)	(24)	--------	--------	--------	--------	--------
Age group IV:															
5	--------	--------	--------	--------	--------	1.7	1.9	2.2	1.8	1.8	1.8	2.1	2.8	3.3	2.8
4	--------	--------	--------	--------	2.1	2.0	2.3	2.5	2.6	2.5	2.8	2.8	3.1	3.0	--------
3	--------	--------	--------	1.7	2.0	1.9	2.0	1.9	1.9	2.1	2.2	2.2	2.2	--------	--------
2	--------	--------	1.0	1.2	1.1	1.2	1.2	.8	1.2	1.2	1.2	1.3	--------	--------	--------
1	--------	.5	.5	.5	.5	.5	.6	.6	.6	.5	.5	--------	--------	--------	--------
Number of fish	--------	(43)	(63)	(54)	(44)	(59)	(39)	(69)	(88)	(61)	(53)	--------	--------	--------	--------
Age group III:															
4	--------	--------	--------	--------	--------	2.5	2.5	2.6	3.1	3.1	2.9	3.8	4.0	4.5	3.8
3	--------	--------	--------	--------	2.5	2.5	2.9	2.6	2.7	2.5	3.2	3.6	4.0	3.2	--------
2	--------	--------	--------	1.3	1.8	1.4	1.4	1.9	2.3	2.7	2.6	3.0	2.3	--------	--------
1	--------	--------	.5	.6	.7	.7	.7	.5	.6	.6	.6	.7	--------	--------	--------
Number of fish	--------	--------	(15)	(21)	(21)	(32)	(20)	(20)	(42)	(46)	(37)	(42)	--------	--------	--------

The range of the percentage fluctuations of growth in weight (table 34) was much greater at each port than was that of growth in length (table 30). This difference is largely due to the nature of the length-weight relation, namely, the increase of weight approximately as the cube of the length. Consequently, the increment of weight corresponding to a particular increment of length depends not only on the amount of growth in length but also on the length of the fish at the time the growth is made. For example, a lake herring that weighs 2 ounces at a length of 8 inches will weigh 4.3 ounces upon reaching a length of 10 inches, a gain of 2.3 ounces. A 10-inch fish that experiences the same 2-inch growth (from 10 to 12 inches) increases its weight from 4.3 to 7.6 ounces, a gain of 3.3 ounces. Both the large size of the fish and the large increments of length contributed to the excellent growth in weight in the more recent years.

The curves of fluctuations of growth in length and weight are further affected by differences with respect to the years of life that exerted greatest influence on the year-to-year percentage changes. Under the procedure of Hile (1941) for estimates of growth fluctuations, the earlier years of life dominated the estimates of fluctuations of growth in length by reason of their larger increments. The data on weight, on the other hand, were least affected at lower ages since the increments of weight were smallest during the earlier years of life. In the later years of life, the weight increments were large when those of length were small.

Similar discrepancies between estimates of fluctuations of growth in length and weight were found by Hile (1954) for walleye and by El-Zarka (1959) for yellow perch in Saginaw Bay.

Table 34.—*Percentage deviation of growth in weight of Lake Superior lake herring from the 1945–59 mean*

Year	Percentage deviation at			Year	Percentage deviation at		
	Bayfield	Portage Entry	Marquette		Bayfield	Portage Entry	Marquette
1945	−28.3	−6.0	−26.8	1953	4.6	−3.4	5.4
1946	−48.4	−6.0	−26.8	1954	2.2	−2.5	4.2
1947	−28.3	−.4	−16.4	1955	11.5	3.8	8.1
1948	−13.6	−9.3	−20.3	1956	19.9	15.2	20.5
1949	−5.7	−6.0	−7.6	1957	16.5	17.1	28.3
1950	−9.9	−12.0	−7.0	1958	26.4	12.7	28.3
1951	11.5	−9.5	−5.7	1959	37.0	12.7	16.0
1952	4.6	−6.6	−.2				

REPRODUCTION

SEX COMPOSITION

Segregation by maturity in the spawning run, in combination with sex differences in age at first maturity and sex differences in the time of arrival of fish on the grounds, limited the use of spawning-run samples for the study of sex composition. The collections from Bayfield in 1959 and 1961 offer examples of the effects of time of capture within the spawning period. A net-run sample collected on November 19, 1959, contained only 3 percent females, and a later sample from the same area on December 8 included 82 percent females. In 1961, net-run samples of lake herring were collected each day the nets were lifted during 15 days of the spawning season (table 35). The number of females exceeded that of the males in all but the first and third days of collection. Had the production of spawning-run fish begun earlier in the season,[3] the percentage of males undoubtedly would have been higher during the first few days. The percentage of females increased steadily after November 23 (exceptions on November 27 and 28) to December 3, when they contributed 93 percent to the total. The advantage of the females decreased slightly in the last 2 days of the season.

Smith (1956) was able to demonstrate differences in the sex ratio according to age, year of collection, depth, season, and gear of capture. His samples from pound nets contained a higher percentage of females in February than during other months; the percentage of females in the samples decreased during 1949–52; the percentage of females decreased with an increase in age in pound net collections and increased with increase in age in gill net collections; in October, females were relatively more plentiful in the deeper than in shallow water.

Table 35.—*Changes in the sex ratio of Lake Superior lake herring during the 1961 spawning season at Bayfield*

[The age groups have been combined]

Date	Number of males	Number of females	Percentage of females
Nov. 20	85	67	44.1
22	87	123	58.6
23	80	75	48.4
24	57	97	63.0
25	57	156	73.2
26	50	150	75.0
27	41	97	70.3
28	53	147	73.5
29	38	155	80.3
30	28	122	81.3
Dec. 1	26	132	83.5
2	21	129	86.0
3	10	132	93.0
4	19	144	88.3
6	23	123	84.2
Combined samples	675	1,849	73.3

Comparable data from Lake Superior did not disclose differences in the sex ratio according to season (with the exception of the spawning season), geographical location, or depth. Since all of the samples came from gill nets, sex data for fish from different gears could not be compared.

The data on sex composition of Lake Superior lake herring were collected during the summer (no fish collected later than September 27 were used in the study of the sex ratio) at: Two Harbors, Minn; Bayfield, Wis.; and Marquette, Mich. The samples for the various dates at these ports were so similar that the collections have been combined (table 36).

The number of females equalled or exceeded that of the males in each age group except the I group (only 1 fish). In the later years, the advantage of the females increased from 52.3 percent for age group III to 81.8 percent for group VII (the percentage dropped to 71.4 percent for age group VIII). For all age groups combined, the percentage of females was 68.5.

Table 36.—*Sex composition of age groups of Lake Superior lake herring*

[Based on summer collections]

Age group	Number of males	Number of females	Percentage of females
I	1		0.0
II	20	20	50.0
III	63	69	52.3
IV	56	146	72.3
V	51	154	75.1
VI	37	87	70.2
VII	8	36	81.8
VIII	4	10	71.4
Combined samples	240	522	68.5

AGE AND SIZE AT MATURITY

Variation is considerable in the age and size at maturity among different populations of lake herring. Most of the lake herring are mature at age group II in the lakes of northeastern Wisconsin (Hile, 1936), Saginaw Bay (Van Oosten, 1929), Green Bay (Smith, 1956), and Lake Erie (Clemens, 1922); at age group III in Lake Ontario (Stone, 1938), Blind Lake, Mich. (Cooper, 1937), Lake Oconomowoc, Wis. (Cahn, 1927), and Lake Superior; and at age group IV in Hudson Bay (Dymond, 1933) and Manitoba Lakes (Bajkov, 1930). Differences in the age and size at maturity often can be correlated with the growth rates of the stocks; fish which have particularly slow growth may mature at a higher age but at a length below that of faster growing specimens (Alm, 1959). This phenomenon was demonstrated among various stocks of whitefish in Lake Superior (Dryer, 1963), but a similar correlation does not appear to exist among all populations of lake herring. Indeed, lake herring from Trout, Silver, and Muskellunge Lakes in northeastern Wisconsin (Hile, 1936) are among the slowest growing for which growth data have been published, but these fish matured at a younger age than those from the faster growing stocks of Lakes Superior and Ontario.

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[3] The fishermen did not start intensive fishing until they could be assured of good catches.

The limited data on the age and size at maturity for Lake Superior lake herring (tables 37 and 38) came from records of nonspawning-run samples. Nearly all of the fish taken in the spawning-run samples were mature. The youngest mature lake herring in Lake Superior belonged to age group II (table 37), and all fish older than the III group were mature. The percentage maturity was higher for males than for females in age groups II and III. All lake herring shorter than 8.5 inches were immature, and all fish longer than 11.9 inches were mature (table 38). The first mature male appeared in the 8.5- to 8.9-inch group and all the males were mature at lengths greater than 11.4 inches. The first mature females appeared in the 9.5- to 9.9-inch group and all were mature at lengths greater than 11.9 inches.

SPAWNING

Spawning of the lake herring in the Great Lakes region takes place some time between mid-November and mid-December. Most investigators agree that water temperature is the main factor influencing the onset of spawning. Various observations and experiments (Cahn, 1927; Pritchard, 1930; Stone, 1938; Brown and Moffett, 1942; Smith, 1956) have shown that spawning does not occur until water temperatures drop below 39.0° F. (3.9° C.).

The earliest spent lake herring from Lake Superior was caught on November 12 in Keweenaw Bay in 1951, and ripe fish were observed as late as December 20 in the Apostle Islands area in 1960. The bulk of the spawning normally takes place during the last week of November and the first week of December. Water temperatures during this time ranged from 40° F. to 37° F. (4.4° C. to 2.8° C.).

Prespawning fish appear on shallow (3 to 6 fathoms) reefs in the Apostle Islands in mid-October. Lake herring are fished commercially on these reefs from mid-October to late Novembe but the catches rarely include spent fish. T fishermen follow the lake herring off the reefs in about 20 fathoms where large-scale spawning fir occurs. As the spawning season progresses, t fishermen move into deeper water and the la large catches are taken from water 60 to fathoms deep. Koelz (1929) stated that spawni lake herring at Marquette were first found in 8 9 fathoms but later moved out to 14 or even 2

TABLE 37.—*Relation between age and sexual maturity of Lake Superior lake herring*

[All fish younger than age group II were immature; all fish older than age group III were mature]

Age group and sex	Number immature	Number mature	Percentage mature
Males:			
II	9	7	44
III	5	22	81
Females:			
II	14	5	26
III	6	20	77

TABLE 38.—*Relation between length and sexual maturity Lake Superior lake herring*

[All fish shorter than 8.5 inches were immature; all fish longer than inches were mature]

Total length (inches)	Males			Females		
	Number immature	Number mature	Percentage mature	Number immature	Number mature	Perce age matu
Inches						
8.5–8.9	1	1	50			
9.0–9.4	4	4	50	4		[illegible]
9.5–9.9	4	4	50	3	1	[illegible]
10.0–10.4	3	6	67	6	3	[illegible]
10.5–10.9		6	100	2	8	[illegible]
11.0–11.4	1	4	80	2	10	[illegible]
11.5–11.9		6	100	1	6	[illegible]

Scanning with the fish magnifier of the dept recorder aboard the *Siscowet* during the 196 spawning season in the Apostle Islands regio confirmed earlier suggestions (Smith, 1956) tha the lake herring are pelagic spawners. Nigh scanning during the peak of the season revealed heavy concentration of fish (presumably lak herring) at 5 to 15 fathoms below the surface i water 35 fathoms deep. A midwater trawl towe 10 fathoms below the surface took small number of lake herring and a 5-foot nylon-cloth, $\frac{1}{16}$-inch mesh net (usually used for the collection of larva fish) towed at 20 fathoms caught small number of lake herring eggs. The eggs undoubtedly wer drifting toward the bottom after release from th fish. Additional evidence of pelagic spawnin comes from the north shore of Lake Superior wher commercial gill nets floated 7 fathoms below th surface in 80 fathoms of water take large number of spawning lake herring.

These findings do not prove that lake herrin are exclusively pelagic spawners. Most of th commercial production from the south shore c the lake comes from nets set on the bottom. Th fish move to the bottom sometime during th night; spawning may continue there.

Evidence from Lake Superior supports earlie findings that spawning lake herring show n preference for a particular bottom type.

FECUNDITY

Fecundity studies of lake herring by earlier authors demonstrated that the number of eggs varied widely according to stock and individuals within a stock. Smith's (1956) detailed account of these findings revealed, in general, that the number of eggs tended to increase with length and weight of the female, but the number of eggs per ounce of body weight decreased with increase in length. The average diameters of eggs from Green Bay lake herring showed no change with increase in length of the female, and the egg diameter and the total number of eggs per individual fish were not correlated.

The fecundity of Lake Superior lake herring was investigated from 30 fully ripe females collected in 1950–54 at Marquette and Portage Entry. The formalin-preserved ovaries were broken up thoroughly and the connective tissue removed. The eggs were then set aside to dry at room temperature for 24 hours or until all signs of moisture had disappeared. A sample of 500 eggs was removed and weighed to the nearest 0.0001 g., and the total number of eggs was computed from their total weight (determined to the nearest 0.0001 g.) and the sample weight.

The dependability of this method was tested by making 14 estimates from 500-egg samples of one pair of ovaries for which an actual count was made. The actual number of eggs counted was 7,523, and the estimates ranged from 7,407 to 7,609. The extreme percentage errors were −1.54 and 1.14. The mean of the absolute values of the percentage errors was 0.63.

The fecundity data for Lake Superior lake herring exhibited identical trends to those described by earlier investigators. The number of eggs tended to increase with fish length, and the number of eggs per ounce of body weight to decrease with increase in length (table 39). The average number of eggs ranged from 4,314 for fish in the 10.6- to 10.8-inch size group to 10,250 for a 14.0-inch fish. The average for the entire sample was 6,351 eggs. The average number of eggs per ounce of body weight ranged from 1,006 for fish in the 10.9- to 11.1-inch size group to 746 for those in the 12.4- to 12.6-inch group. The average number of eggs per ounce of fish for the entire sample was 842.

Comparable data from Lake Superior and Green Bay (Smith, 1956) reveal that the Lake Superior lake herring typically produce fewer eggs per individual fish and fewer eggs per ounce of fish weight (table 40). The production of eggs from individual Green Bay lake herring was larger for each length interval for which comparable data were available (exception at 11.5 to 11.7 inches). The number of eggs per ounce of fish was also higher for Green Bay lake herring in 4 of 6 comparisons. The unweighted means for each sample showed that Green Bay lake herring produced over 1,000 more eggs per individual fish and nearly 100 more eggs per ounce of fish.

The egg diameters of Lake Superior lake herring were measured for only one 11.4-inch female.

TABLE 39.—*Relation between the length of Lake Superior lake herring and the total number of eggs and the number per ounce of weight*

[Number of fish in parentheses]

Total length	Number of eggs per fish		Average number of eggs per ounce of fish
	Average	Range	
(Inches)			
10.6–10.8	4,314 (2)	3,834–4,794	828
10.9–11.1	5,802 (4)	3,728–9,417	1,006
11.2–11.4	5,354 (4)	4,515–6,922	896
11.5–11.7	6,719 (7)	4,712–8,579	978
11.8–12.0	5,425 (4)	4,735–5,912	787
12.1–12.3	6,075 (3)	5,310–7,514	792
12.4–12.6	5,495 (2)	5,305–5,684	746
12.7–12.9	7,726 (3)	6,970–8,685	793
13.9–14.1	10,250 (1)		754
All lengths	6,351 (30)	3,728–10,250	842 (30)

TABLE 40.—*Number of eggs per fish and per ounce of weight produced by lake herring of Green Bay (Lake Michigan), and Lake Superior*

[The data for Green Bay are from Smith (1956). Number of fish in parentheses]

Total length	Average number of eggs per fish		Average number of eggs per ounce of fish	
	Green Bay	Lake Superior	Green Bay	Lake Superior
(Inches)				
10.6–10.8	6,662 (15)	4,314 (2)	1,156 (16)	828 (2)
10.9–11.1	6,079 (16)	5,802 (4)	976 (15)	1,006 (4)
11.2–11.4	5,790 (14)	5,354 (4)	918 (11)	896 (4)
11.5–11.7	6,140 (11)	6,719 (7)	851 (9)	978) (4)
11.8–12.0	7,663 (4)	5,425 (4)	986 (3)	787 (4)
12.1–12.3	8,109 (1)	6,075 (3)	977 (1)	972 (3)
All lengths [1]	6,741	5,615	977	881

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[1] Unweighted means.

The mean diameter of 48 eggs was 1.88 mm., exactly that found by Smith (1956) from 20 specimens taken in November in Green Bay.

FOOD HABITS

Stomach contents were examined from 146 lake herring collected on various dates in 1950–60 at Bayfield, Wis., and Marquette, Mich. (table 41).

Crustacea, found in 83 percent of the stomachs examined were by far the most common food of lake herring. Copepods (*Diaptomus*, *Epischura*, and *Limnocalanus*) were found in all of the stomachs of small lake herring (5.6–6.4 inches) in the May sample, in 93 percent of the stomachs of the June–July and September–October collections, and in 66 percent of the stomachs of the December sample. The total frequency of occurrence for copepods was 71 percent. Cladocera (*Daphnia*) ranked second (36 percent), and Mysidacea (*Mysis relicta*), important only in the December sample, were in 19 percent of the total stomachs examined.

Insects were not found in the May or December collections but were in 61 percent of the June–July samples and in 23 percent of the September–October collections. Of the insects that were positively identified, Formicidae and Diptera
most common.

TABLE 41.—*Food in stomachs of Lake Superior lake herring collected at Bayfield and Marquette, 1950–60*

Item	Percentage occurrence in seasonal samples				All dates
	May 3, 1960	June 6–July 30, 1959	Sept. 17, 1958 Sept. 30–Oct. 2, 1959	Dec. 5, 1950	
Number of stomachs	5	43	43	55	146
Length of fish [1]	5.6–6.4	4.3–13.0	5.3–16.5	11.0–12.9	5.6–16.5
Food item:					
Crustacea (total)	100	93	93	66	83
Copepoda	100	84	58	10	71
Cladocera	---------	44	74	2	36
Mysidacea	---------	9	5	40	19
Amphipoda	---------	---------	---------	2	2
Unidentified remains	---------	12	19	33	21
Insecta (total)	---------	61	23	---------	25
Formicidae	---------	7	---------	---------	2
Diptera	---------	7	5	---------	4
Lepidoptera	---------	2	---------	---------	1
Homoptera	---------	2	---------	---------	1
Hymenoptera [2]	---------	2	---------	---------	1
Hemiptera	---------	-- 2	---------	---------	1
Thysanoptera	---------	2	---------	---------	---------
Unidentified remains	---------	33	19	---------	15
Pelecypoda	---------	---------	2	---------	1
Rotatoria	---------	2	2	6	3
Hydracarina	---------	---------	2	2	1
Fish remains	---------	---------	---------	2	1
Fish eggs	---------	---------	---------	62	23
Chlorophyta	40	72	---------	4	24
Diatoms	---------	35	7	---------	12
Unidentified debris	---------	7	12	35	19

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[1] Total length, inches.
[2] Exclusive of the ants.

Fish eggs (lake herring) were found in 62
cent of the stomachs in the December san
Although the lake herring is known to prey o
own eggs, a question arises as to whether
herring eggs are a preferred food or if they
eaten incidentally with plankton. Since the m
foods of the lake herring are pelagic, the eggs
simply be eaten as they drift toward the bot
after being released by pelagic spawners. S
eggs could, of course, have been taken from
bottom. The consumption of fingernail clams
water mites, though rare, gives evidence of o
sional bottom feeding.

The common food found in the lake herr
stomachs during various seasons of the year gi
strong support to the belief that the lake herr
is primarily pelagic.

DISTRIBUTION

The seasonal distribution of the lake herr
has been a subject of considerable speculat
among fishermen as well as researchers. Th
the fish disappear in Lake Superior during
summer cannot be disputed. Prior to 19
the only summer fishery for lake herring on
lake existed along the north shore and at I
Royale where floated nets yielded small catch

A small summer lake herring fishery develop
in 1960–62 at Marquette where bottom nets s
at about 20 fathoms produced some good catch

Koelz (1929) caught only a few stragglers
his experimental nets at depths of 10 to 1
fathoms during the summer in Lake Superi
and reported that fishermen believed they h
seen schools of lake herring near the surface
the open lake at that season.

In the course of the 1958–61 studies of fis
populations in western Lake Superior by th
research vessel *Siscowet*, special cruises collecte
information on the seasonal changes in the are
and depth distribution of the lake herrin
Experimental fishing was carried out in sever
locations among the Apostle Islands with standa
gill nets (300 feet each of 2- to 2¾-inch mesh
bull nets (gill nets 300 feet long, 100 meshes dee
with mesh sizes of 2⅜ and 2½ inches), and botto
and midwater trawls. The bottom trawls were
semiballoon type with a 31-foot headrope, 2

TABLE 42.—*Number of lake herring caught per 1,000 linear feet of 2- to 2¾-inch-mesh gill nets set on the bottom at various depths in western Lake Superior, 1958–61*

[Number of lifts in parentheses]

Time period and item	Depth of water (fathoms)								
	<10	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89
pril 27–June 30 Number of fish	5 (3)	8 (11)	12 (21)	11 (6)	0 (2)	4 (15)	2 (4)	0 (4)	3 (4)
uly 1–Sept. 13 Number of fish	0 (2)	8 (22)	10 (21)	1 (5)	3 (14)	3 (6)	7 (1)	-----	2 (2)
ept. 14–Oct. 14 Number of fish	13 (3)	35 (16)	4 (18)	2 (3)	0 (4)	0 (1)	0 (2)	7 (2)	-----
ct. 15–Nov. 15 Number of fish	85 (22)	0 (2)	4 (3)	23 (1)	-----	19 (4)	-----	-----	-----
ov. 16–Dec. 20 Number of fish	287 (7)	330 (2)	42 (3)	98 (3)	201 (2)	284 (7)	280 (3)	-----	66 (4)

nch-mesh body, and ½-inch-mesh cod end. The midwater trawl was converted from a bottom trawl o full-balloon type and was equipped with trawl lane floats. The standard gill nets were fished n the bottom at depths of 2 to 89 fathoms, and he bull nets were floated at different depths below he surface or set obliquely from the surface to the ottom. The floating and "oblique" nets were uspended at the desired distance below the surace from a series of floats. A limited amount of rift-netting (nets attached to unanchored boat, llowed to drift freely) was carried out in various arts of the open lake but few lake herring were aptured. The bottom trawls were fished at 5 to 0 fathoms, and the midwater trawl was employed hen pelagic schools of fish were observed on the ensitive echo-sounder aboard the vessel. The ata gained from this experimental fishing failed y far to bring out clearly the movements and istribution of the lake herring, but they did add materially to the hitherto negligible information on the subject.

Some explanations are required to permit an instructive account of the depth distribution of lake herring in Lake Superior from the records of tables 42 and 43. The time covered may be subdivided according to seasonal thermal conditions and the spawning season. Prior to July 1, the water of western Lake Superior was generally homothermous although surface temperatures occasionally reached 50° F. in late June. The surface water began to warm fairly rapidly in early July, and a pronounced thermocline soon developed. This condition persisted until about mid-September when the early fall storms mixed the water and the depth of the epilimnion increased to 80–100 feet. By mid-November (the beginning of the spawning season) the water was again almost homothermous at temperatures of about 43° F.

The depths listed in table 42 are the depths of water in fathoms where the nets were set; the nets fished 1 fathom of water immediately above the bottom. In table 43, the listed depths show the range and mean (in fathoms) that the bull nets were fished below the surface. The change of catch with the depth the nets were fished below the surface did not vary with the maximum depth of the water.

The catch of lake herring from gill nets set on the bottom was small at all depths and periods except during the spawning season (table 42). During April 27–June 30, the largest catch was only 12 fish per 1,000 linear feet (taken at 20–29 fathoms). At no depths below 39 fathoms did the catch exceed four fish. Between July 1 and

ABLE 43.—*Number of lake herring caught per 1,000 linear feet of 2⅜- and 2½-inch-mesh bull nets fished at various depths below the surface in western Lake Superior, 1958–60*

[Number of lifts in parentheses. Temperatures ° F.]

Time period and item	Depth of water fished (fathoms)—range and mean (in parentheses)								
	<6.5 (3.3)	3.3–9.8 (6.6)	6.7–13.2 (10.0)	10.0–16.5 (13.3)	13.3–19.8 (16.6)	16.7–23.2 (20.0)	20.0–26.5 (23.3)	23.3–29.8 (26.6)	26.7–33.2 (30.0)
lay 17–June 30:									
Number of fish	51	29	20	-----	-----	-----	-----	-----	-----
Average temperature	46°	42°	39°	-----	-----	-----	-----	-----	-----
	(4)	(4)	(1)	-----	-----	-----	-----	-----	-----
ly 1–Sept. 13:									
Number of fish	19	27	25	23	7	2	4	4	0
Average temperature	67°	56°	45°	42°	41°	39°	39°	39°	39°
	(13)	(9)	(7)	(7)	(5)	(4)	(6)	(4)	(3)
pt. 14–Oct. 5:									
Number of fish	140	127	133	110	104	50	12	17	2
Average temperature	55°	55°	55°	52°	47°	45°	44°	42°	44°
	(6)	(13)	(8)	(9)	(9)	(6)	(6)	(4)	(3)

September 13, few lake herring were captured, all at depths below 10 fathoms. The data suggest a widely scattered distribution between 10 and 69 fathoms during this period. In the early fall (September 14–October 14), most of the lake herring were taken in the 10- to 19-fathom stratum; they disappeared almost entirely at depths below 39 fathoms (exception was the catch of 7 fish per 1,000 linear feet of net at 70–79 fathoms). The prespawning fish began to concentrate on shallow reefs in October 15–November 15. Small-mesh gill nets set on the lake trout spawning reefs (3 to 6 fathoms) during mid-October often caught large numbers of lake herring which were nearly ripe. The period November 16–December 20 (which includes the lake herring spawning season) yielded relatively large numbers of lake herring at all depths. (The small numbers of fish taken at 20–39 fathoms is misleading because these sets were made for another species on grounds not frequented by lake herring.)

Water temperatures on the bottom were relatively low during all seasons. The highest temperature (53.5° F.) was recorded at 15 fathoms on September 30, and the lowest (34.9° F.) was at 24 fathoms on December 13.

Because the small catches of lake herring in the bottom nets suggest a pelagic life for the species, a better description of their depth distribution should be obtained from the records of catches from floating and "oblique" sets of bull nets (table 43). During May 17–June 30, the lake herring were most abundant (51 per 1,000 linear feet) at depths less than 7 fathoms. The catch of 29 fish at 3–10 fathoms and 20 fish at 7–13 fathoms suggested a decrease in abundance with an increase in depth. The average water temperature during this period ranged from 46° F. at 3 fathoms to 39° F. at 10 fathoms. No sets were made below 13 fathoms during the period. From July 1 to September 13 the largest numbers of lake herring were caught at 3–17 fathoms. The decrease in the number of fish between the surface and 7 fathoms may be the result of relatively high water temperatures in the surface layers (67° F.). Good catches of lake herring were rare in water warmer than 60° F. Lake herring were scarce below 17 fathoms. Since the lake herring are principally plankton feeders during the summer and the heaviest concentration of plankton occurs in the upper water levels, their depth distribution may be determined by the abundance of fo
various depths. On July 9, 1959, the *Sis*
collected several plankton samples with a
of Clarke-Bumpus plankton samplers towed
7, and 20 fathoms below the surface. The
centration of plankton at 2 fathoms was extre
heavy; it was much lighter at 7 fathoms, ar
20 fathoms practically no plankters were captu

The best catches in the bull nets were r
during September 14–October 5. At this
the fish were abundant at depths to 20 fath
(140 fish per 1,000 linear feet at 0–7 fathom
104 fish at 13–20 fathoms). The increase in
catch in the shallowest water followed a decr
in average water temperature to 55° F. The
at this time apparently were moving toward
inshore areas prior to the late-fall spawning.

The catch of lake herring in bottom trawls
practically nil regardless of season, depth,
temperature of water. The midwater trawl to
10 fathoms below the surface at night during
spawning season took only small numbers of l
herring.

The data from the catches of bottom nets
bull nets suggest that the vertical distributio
the lake herring may be influenced by temperat
abundance of plankton, and spawning. V
little is known of the horizontal movements
the species, although the available evidence in
cates a random areal distribution in the insh
areas during April–June, a wide scattering dur
the summer (possibly small scattered schools
the open lake), an inshore movement in early
when the fish begin to form larger schools
advance of spawning, and finally, the spawni
season when they can be caught at widely var
depths and locations. Our recorded catches w
affected, to be sure, by changes in activity as w
as numbers. Heightened activity was probab
an important factor in the fall catches, especia
in the spawning season.

SUMMARY

1. The lake herring has been the princip
species in the commercial production of La
Superior since 1908. The 1929–61 average annu
catch in U.S. waters was nearly 12 million pound
62.4 percent of the total U.S. production of la
herring for the Great Lakes. Minnesota dom
nated the catch in 1929–40, Wisconsin held t

ead in 1941–56 (exception in 1942), and Michigan had the largest catch in 1942 and 1957–61.

2. Small-mesh gill nets (2¼- to $2\frac{7}{16}$-inch mesh) are the principal gear for catching lake herring n Lake Superior. On the average, about 90 percent of the annual production is landed during the spawning season in November and December.

3. Although recent production of lake herring n U.S. waters is not significantly below the 1929–31 mean, evidence exists that abundance has declined in certain areas of the lake. The decline rom 1950–55 to 1956–61 in numbers of fish caught per unit effort of fishing was 31 percent at Bayfield and Portage Entry, and 27 percent at Marquette.

4. The life-history studies were based on 12,187 lake herring collected from commercial and experimental gill nets fished at various locations in Lake Superior in 1950–62. Individual growth histories were computed for 3,779 specimens collected from commercial landings at: Duluth, Minn.; Bayfield, Wis.; and Portage Entry and Marquette, Mich., during the fall spawning seasons of 1950–59. Growth was computed from scale measurements by direct proportion. Fish used in other phases of the study came from experimental gill nets and rom the summer commercial lake herring fishery.

5. Some fish had begun new growth by May 3, although annulus formation was not complete until mid-August. Over 90 percent of the season's growth was complete by the end of September.

6. The age composition and mean age of the commercial samples varied moderately by year of capture and port. Age group IV dominated the catch each year at each port and contributed 53.2 percent of the total, followed by age group III (24.8 percent) and age group V (18.4 percent). The remaining age groups (II, VI, and VII) combined, contributed only 3.6 percent. The mean age of all the years' collections was 3.9 at Bayfield, Portage Entry, and Marquette, and 4.1 at Duluth. With few exceptions the average age of the females exceeded that of the males. The differences between the mean ages of the sexes did not exceed 0.5 year.

7. Although estimates of year-class strength were affected by several sources of bias, a ranking was nevertheless made on the basis of the number of fish of various ages taken per unit effort of fishing. The strength of the year classes declined rregularly at all of the ports during the period (1946–55) for which data were available. The values (given as percentage deviations from the mean) ranged from 55.9 in 1947 to −44.0 in 1954 at Bayfield, from 55.7 in 1950 to −40.8 in 1955 at Portage Entry, and from 40.7 in 1947 to −33.7 in 1952 at Marquette. Fluctuations of year-class strength were similar at Marquette and Bayfield. Only the 1947 and 1950 year classes showed better than average strength at each port. Year classes 1954 and 1955 were weak at all ports.

8. The average total length of the females of an age group at capture was longer than that of the males in 20 of 24 comparisons at Duluth, Bayfield, and Portage Entry, and the males held a slight advantage (7 of 10 comparisons) at Marquette.

9. With only one exception (that of the VI-group males in the 1956–59 Bayfield samples), the average length of the age groups was larger in 1956–59 than in 1950–55. The increase in average length from the early to the late period ranged from 0.4 inch for the V-group males at Bayfield to 1.1 inches for the V-group males at Portage Entry. In general, the average size of the lake herring increased from the western to the eastern part of the lake.

10. The length distributions of the age groups typically had small ranges and extensive overlap. The length range of the age groups in the 1957 Marquette sample, for example, were as small as 1.9 inches (age group II) and did not exceed 3.9 inches (VI-group fish). The length interval of 12.0–13.4 inches was represented by all five age groups.

11. The relation between the total length in inches (L) and the weight in ounces (W) of Lake Superior lake herring from all of the collections, was described by the equation, $\log W = -2.54688 + 3.17008 \log L$.

12. The weights of lake herring of corresponding lengths were heavier in 1956–61 than in 1950–55. The average percentage increase in weight, length for length, was 8.8 percent at Bayfield, 5.2 percent at Marquette, and 4.4 percent at Portage Entry. Port-to-port differences in average weight among fish of the same length in 1950–55 showed a west-to-east trend toward increased weight. In 1956–61 the Marquette lake herring were generally heaviest, but port-to-port differences in weight among fish from Duluth, Bayfield, and Portage Entry were small.

13. The growth rate of Lake Superior lake herring varied according to port and period of capture. The fish from Duluth in 1956–59 were the slowest growing, followed in rank by those from Bayfield, Portage Entry, and Marquette. With only one exception (that of first-year calculated lengths of the Portage Entry fish), the calculated lengths of lake herring taken in 1956–59 were greater than those of fish taken in 1950–55. Lake herring caught in the later period at Marquette ranged from 0.2 inch longer in the first to 1.3 inches longer in the seventh year of life. Growth in length was greatest during the first year of life in both collecting periods (from 4.3 inches at Duluth to 5.0 inches at Marquette in 1956–59). With few exceptions, the annual increments of growth in length decreased progressively until the fifth year of life, after which the increments were 1.0 inch or less.

14. Growth in weight also increased from the western to eastern ports and from the early to late collecting period. The first-year calculated increments were small (less than 0.7 ounce) in both collecting periods. The increments increased progressively to a maximum in the fourth year of life at all ports except Bayfield and Marquette in 1956–59, where the annual increments were highest in the seventh year of life. The largest increment in weight (2.9 ounces) was in the seventh year of life at Marquette in 1956–59.

15. The trends of annual fluctuations in growth in length were similar at the three ports. In general, growth was below average in 1945–53 and above average in 1954–59. The quality of growth for all years of life expressed as percentage deviation from the 1945–59 mean, ranged from a low of −23.5 at Bayfield in 1946 to a maximum of 16.3 at Bayfield in 1959.

16. The annual fluctuations of growth in weight were similar to those of growth in length. Growth in weight was below average at Bayfield in 1945–50, at Portage Entry in 1945–54, and at Marquette in 1945–52. Growth was above average at all of the ports after 1954.

17. No correlation could be established between fluctuations of growth and changes in temperature or the abundance of lake herring.

18. The number of females equalled or exceeded that of the males in each age group except I (only 1 fish) from the nonspawning-run samples. The advantage of the females progressively increased from 52.3 percent for age group III to 81.8 percent for group VII. The percentage of females was 68.5 for all age groups combined.

19. The youngest mature lake herring in Lake Superior belonged to age group II, and all fish older than III were mature. The shortest mature male appeared in the 8.5- to 8.9-inch group, and all males were mature at lengths greater than 11.4 inches. The first mature females appeared at 9.5–9.9 inches, and all were mature at lengths greater than 11.9 inches.

20. Major spawning of Lake Superior lake herring normally takes place during the last week of November and the first week of December. Water temperature at this time usually is between 37° F. and 40° F. The fish are pelagic spawners; the eggs are broadcast and settle to the bottom at depths ranging from 20 to 80 fathoms. The spawning fish show no preference for a particular bottom type.

21. The number of eggs produced by female lake herring (range 4,314 to 10,250) tended to increase with fish length, and the number of eggs per ounce of body weight decreased with increase in length. Lake Superior lake herring typically produce fewer eggs per individual fish and fewer eggs per ounce of fish weight than do lake herring from Green Bay, Lake Michigan.

22. Crustacea were by far the most common food and were found in 83 percent of 146 stomachs examined from Lake Superior lake herring. Other food included insects and fish eggs (presumably those of lake herring).

23. The vertical distribution of the lake herring may be influenced by temperature, abundance of plankton, and spawning. During the early summer, the fish are most common near the surface where plankton is most abundant. As the surface water warms in midsummer, the lake herring move to deeper levels, despite the high concentration of plankton near the surface. After September 13, they were randomly distributed from the surface to about 20 fathoms, and during the spawning season, they were captured in good numbers at all depths down to 90 fathoms.

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LITERATURE CITED

ALM, GUNNAR.

1959. Connection between maturity, size and age in fishes. Fishery Board of Sweden, Report of the Institute of Freshwater Research, Drottningholm, No. 40, pp. 5–145.

BAJKOV, ALEXANDER.

1930. Fishing industry and fisheries investigations in the prairie provinces. Transactions of the American Fisheries Society, vol. 60, pp. 215–237.

BROWN, C. J. D., AND J. W. MOFFETT.

1942. Observations on the number of eggs and feeding habits of the cisco (*Leucichthys artedi*) in Swains Lake, Jackson County, Michigan. Copeia, 1949, No. 3, pp. 149–152.

CAHN, ALVIN ROBERT.

1927. An ecological study of southern Wisconsin fishes. Illinois Biological Monographs, vol. II, No. 1, 151 pp.

CARLANDER, KENNETH D.

1945. Growth, length-weight relationship and population fluctuations of the tullibee, *Leucichthys artedi tullibee* (Richardson), with reference to the commercial fisheries, Lake of the Woods, Minnesota. Transactions of the American Fisheries Society, vol. 73 (1943), pp. 125–136.

CLEMENS, WILBERT A.

1922. A study of the ciscoes of Lake Erie. University of Toronto Studies, Biological Series, No. 20, Publications Ontario Fisheries Research Laboratory, No. 2, pp. 27–37.

COOPER, GERALD P.

1937. Age, growth, and morphometry of the cisco, *Leucichthys artedi* (Le Sueur), in Blind Lake, Washtenaw County, Michigan. Papers Michigan Academy of Science, Arts, and Letters, vol. 22 (1936). pp. 563–571.

DEASON, HILARY J., AND RALPH HILE.

1947. Age and growth of the kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Transactions of the American Fisheries Society, vol. 74 (1944), pp. 88–141.

DRYER, WILLIAM, R.

1963. Age and growth of the whitefish in Lake Superior. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 63, No. 1, pp. 77–95.

DYMOND, J. R.

1933. Biological and oceanographic conditions in Hudson Bay. The coregonine fishes of Hudson and James Bays. Biological Board of Canada, Contributions Canadian Biology and Fisheries, vol. 8, No. 1 (series A, general, No. 28), pp. 1–12.

EL-ZARKA, SALAH EL-DIN.

1959. Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill), in Saginaw Bay; Lake Huron. U.S. Fish and Wildlife Service, Fishery Bulletin 151, vol. 59, pp. 365–415.

HILE, RALPH.

1936. Age and growth of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bulletin of the U.S. Bureau of Fisheries, No. 19, vol. 48, pp. 211–317.

1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters, vol. 33, pp. 189–337.

1954. Fluctuations in growth and year-class strength of the walleye in Saginaw Bay. U.S. Fish and Wildlife Service, Fishery Bulletin 91, vol. 56, pp. 7–59.

HJORT, JOHAN.

1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux, Conseil Permanent International pour l'Exploration de la Mer, vol. 20, 288 pp.

HUBBS, CARL L., AND KARL F. LAGLER.

1958. Fishes of the Great Lakes Region. The Cranbrook Institute of Science, Bloomfield Hills, Michigan, Bulletin 26, 213 pp. (revised edition).

JOBES, FRANK W.

1952. Age, growth, and production of yellow perch in Lake Erie. U.S. Fish and Wildlife Service, Fishery Bulletin 70, vol. 52, pp. 205–266.

KOELZ, WALTER N.

1926. Fishing industry of the Great Lakes. Department of Commerce, Report of the U.S. Commissioner of Fisheries for 1925, Appendix II, pp. 553–617.

1929. Coregonid fishes of the Great Lakes. Bulletin of the U.S. Bureau of Fisheries, vol. 43 (1927), part 2, pp. 297–643.

MOFFETT, JAMES W.

1952. The study and interpretation of fish scales. The Science Counselor, vol. 15, No. 2, pp. 40–42.

PRITCHARD, ANDREW L.

1930. Spawning habits and fry of the cisco (*Leucichthys artedi*) in Lake Ontario. Biological Board of Canada, Contributions Canadian Biology and Fisheries, N.S., vol. 6 (1930), No. 9, pp. 227–240.

PYCHA, RICHARD L.

1961. Recent changes in the walleye fishery of northern Green Bay and history of the 1943 year class. Transactions of the American Fisheries Society, vol. 90, No. 4, pp. 475–488.

SCOTT, W. B.

1951. Fluctuations in abundance of the Lake Erie cisco (*Leucichthys artedi*) population. Contributions Royal Ontario Museum of Zoology, No. 32, 41 pp.

SMITH, STANFORD H.

1954. Method of producing impressions of fish scales without using heat. U.S. Fish and Wildlife Service, Progressive Fish-Culturist, vol. 16, No. 2, pp. 75–78.

1956. Life history of lake herring of Green Bay, Lake Michigan. U.S. Fish and Wildlife Service, Fishery Bulletin 109, vol. 57, pp. 87–138.

Stone, Udell B.

1938. Growth, habits, and fecundity of the ciscoes of Irondequoit Bay, New York. Transactions of the American Fisheries Society, vol. 67 (1937), pp. 234–245.

Van Oosten, John.

1929. Life history of the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. Bulletin of the U.S. Bureau of Fisheries, vol. 44 (1928), pp. 265–428.

1944. Factors affecting the growth of fish. Transactions of the Ninth North American Wildlife Conference, pp. 177–183.

Van Oosten, John, and Ralph Hile.

1949. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in Lake Erie. Transactions of the American Fisheries Society, vol. 77 (1947), pp. 176–249.

Watt, Kenneth E. F.

1956. The choice and solution of mathematical models for predicting and maximizing the yield of a fishery. Journal of the Fisheries Research Board of Canada, vol. 13, No. 5, pp. 613–645.

ANNOTATED BIBLIOGRAPHY ON BIOLOGY OF MENHADENS AND MENHADENLIKE FISHES OF THE WORLD

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ABSTRACT

The bibliography has 238 references on the classification, distribution, abundance, ecology, and life history of menhadens and similar clupeid fishes of the genera *Brevoortia, Ethmalosa,* and *Ethmidium.* Included are major references to the North American menhaden articles published through 1957 and all references 1958–62. All available references to the South American menhadens and the West African shad are included. Brief annotations and a subject index also are provided.

This bibliography is an expansion and a continuation of that compiled by Reintjes, Christmas, and Collins (1960) on the biology of the American menhadens. Of the literature listed in that publication pertaining to the North American menhadens, only the major references published before 1958 are included in this work; the minor references, checklists, and incidental reports are not. Any references published prior to 1958 that were omitted from the preceding bibliography are included.

The bibliography concerns the menhadens, genus *Brevoortia,* and similar clupeid or menhadenlike fishes of the genera *Ethmalosa* and *Ethmidium.* At present, *Brevoortia,* on the Atlantic Coast of the United States including the Gulf of Mexico, and *Ethmalosa,* on the Atlantic Coast of West Africa, compose the largest fishery in each area. Furthermore, *Brevoortia* and *Ethmidium* offer resource potentials for the Atlantic and Pacific Coasts of South America.

Knowledge of the scientific and technical information on the identity, distribution, and biology of these fishes is essential for determining the extent of their resources and their potential. The principal purpose of this bibliography is to encourage inquiry, research, and exploration, by furnishing references to the published accounts on menhaden and menhadenlike fishes.

In general, the geographical distribution of the species of menhadens and menhadenlike fishes of the world[1] may be summarized as shown in table 1.

In reviewing the literature, certain criteria were used to decide which references should be included. Included, in general, were references to taxonomy, distribution, occurrence, abundance, life history, morphology, ecology, and behavior. Excluded generally were references on the technological aspects of the fishery and the processing industry; daily, monthly, and annual landing reports and statistics; popular accounts in trade journals, newspapers, and magazines; and administrative and project reports. Mimeographed or similarly processed reports of an established series, or when principally concerned with these fishes, have been included.

The arrangement of the references is alphabetically by author's surname. With multiple authors the entry is made only under the senior author's name. Each author's works are listed chrono-

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[1] The genera *Macrura, Gudusia,* and *Hilsa* (in part) from the Indian Ocean, although similar, are not included in this bibliography.

TABLE 1.—*Menhadens and menhadenlike fishes by geographical areas*

Scientific name	Common name	Area
Brevoortia tyrannus	Atlantic menhaden	Atlantic Coast of North America from Nova Scotia to Florida.
Brevoortia smithi	Yellowfin menhaden	Atlantic Coast of the United States and Gulf of Mexico from North Carolina to Louisiana.
Brevoortia patronus	Gulf menhaden	Gulf of Mexico from Florida to Mexico.
Brevoortia gunteri	Finescale menhaden	Gulf of Mexico from Alabama to Mexico.
Brevoortia pectinata	Lacha or savelha	Atlantic Coast of South America from Brazil to Argentina.
Brevoortia aurea	Lacha or savelha	Atlantic Coast of South America from Brazil to Argentina.
Ethmidium chilcae	Machete, machuela, or trite.	Pacific Coast of South America from Peru and Chile.
Ethmidium maculatum	Machete, machuela, or trite.	Pacific Coast of Central and South America from Mexico to Peru.
Ethmalosa fimbriata	West African shad or bonga.	Atlantic Coast of West Africa from Senegal to Angola.

logically by year of publication, and those published in the same year are given alphabetical sequence by title. Pagination is given for the complete paper, not solely for the pages referring directly to the subject species. Such a restricted pagination was used by Reintjes, Christmas, and Collins (1960) to circumscribe limited references to menhaden occurring incidentally in larger works.

Brief annotations of the contents of the publications and the scientific names of the species concerned are given. This annotation is done not to make value judgments of the papers but to give clearer descriptions of the contents than can be obtained from their titles.

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BIBLIOGRAPHY

ABBOTT, JAMES FRANCIS.

1899. The marine fishes of Peru. Proceedings of the Academy of Natural Sciences, Philadelphia, vol. 51, pt. 2, pp. 324–364.

Potamalosa notacanthoides and *P. maculata* described.

ANDERSON, ARTHUR E., EDWARD C. JONAS, and HOWARD T. ODUM.

1958. Alteration of clay minerals by digestive processes of marine organisms. Science, vol. 127, No. 3291, pp. 190–191.

Clay minerals in stomach contents of menhaden mentioned.

ANGELESCU, VICTOR, and ENRIQUE E. BOSCHI.

1959. Estudio biologico pesquero del langostino de Mar del Plata en conexión con la Operacion Nivel Medio. Republica Argentina, Secretaria de Marina, Servicio de Hidrografia Naval, H. 1017, 135 pp.

Brevoortia aurea taken by shrimp trawls in the region of Mar del Plata.

ANONYMOUS.

1948. Note on *Ethmalosa fimbriata* (Bowdich). Cybium, Fiche Ichtyologique, No. 2, pp. 5–7; No. 3, pp. 7–8.

Vernacular names in West Africa.

1959. Menhaden—research on parasites may reveal migratory routes. U.S. Department of the Interior, Fish and Wildlife Service, Commercial Fisheries Review, vol. 21, No. 6, p. 40.

A brief comment on the use of parasites as natural tags to infer menhaden migrations.

ARNOLD, EDGAR L., JR., RAY S. WHEELER, and KENNETH N. BAXTER.

1960. Observations on fishes and other biota of East Lagoon, Galveston Island. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 344, 30 pp.

Monthly occurrence of *Brevoortia patronus* larvae, 1953–58.

ARVE, JOHN.

1960. Preliminary report on attracting fish by oyster-shell plantings in Chincoteague Bay, Maryland. Chesapeake Science, vol. 1, No. 1, pp. 58–65.

Brevoortia tyrannus caught in wire fish traps.

BAILEY, REEVE M., ERNEST A. LACHNER, C. C. LINDSEY, C. RICHARD ROBINS, PHIL M. ROEDEL, W. B. SCOTT, and LOREN P. WOODS.

1960. A list of common and scientific names of fishes from the United States and Canada. American Fisheries Society, Special Publication No. 2, 102 pp.

Common and scientific names of the four North American species of *Brevoortia*.

BAINBRIDGE, V.

1957. Food of *Ethmalosa dorsalis* (Cuvier and Valenciennes). Nature, vol. 179, No. 4565, pp. 874–875.

Comparison of food contents of *Ethmalosa dorsalis* with plankton and relation to salinity of Sierra Leone River.

1960. The plankton of inshore waters off Freetown, Sierra Leone. British Colonial Office, Fishery Publication No. 13, 48 pp.

Relation of the plankton to the *Ethmalosa* or bonga fishery.

1961. The early life history of the bonga, *Ethmalosa dorsalis* (Cuvier and Valenciennes). Journal du Conseil, vol. 26, No. 3, pp. 347–353.

Description of developing eggs and newly hatched

larvae of *Ethmalosa dorsalis* from eggs artificially fertilized, and the occurrence of eggs and larvae in Sierra Leone River.

1962. The larvae of *Pellonula vorax* (Günther) (Clupeidae) in Sierra Leone coastal waters. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 24, No. 1, p. 262–269.

Includes a comparison of *Ethmalosa dorsalis* with other clupeid larvae (*Pellonula vorax*, *Sardinella eba*, *S. cameronensis*, and *Ilisha africana*).

BEARDEN, CHARLES M.

1961. Common marine fishes of South Carolina. Contributions from Bears Bluff Laboratories, No. 34, 47 pp.

Brevoortia tyrannus listed.

BEATTY, STANLEY A.

1959. Report to the Government of Brazil on the organization of fish processing research. Food and Agriculture Organization of the United Nations, Expanded Technical Assistance Program, Report No. 1174, 41 pp.

Reported *Brevoortia tyrannus* "savelha" among the principal species salted in the Rio Grande area.

1961. Brazilian fishing. *In* Georg Borgstrom and Arthur J. Heighway, editors, Atlantic Ocean fisheries, pp. 205–212. Fishing News (Books) Ltd., London.

Brief comments on the fishery for *Brevoortia tyrannus aurea*.

BEHNKE, ROBERT J., and RALPH M. WETZEL.

1960. A preliminary list of the fishes found in the fresh waters of Connecticut. Copeia, 1960, No. 2, pp. 141–143.

Brevoortia tyrannus listed from fresh water.

BERG, CARLOS.

1895. Enumeración sistemática y sinonímica de los peces de las costas Argentina y Uruguaya. Anales del Museo Nacional de Historia Natural de Buenos Aires, tomo 4, serie 2, pp. 1–120.

Clupea pectinata and *Brevoortia tyrannus* listed with synonymy.

BERG, LEO S.

1940. Sistema ryboobraznykh i ryb, nyne zhivushchikh i iskopaemykh. Akademii͡a Nauk SSSR, Trudy Zoologicheskogo Instituta, Moskva, tom 5, vyp. 2, 345 pp.

Classification of genera *Brevoortia* and *Ethmidium*.

1947. Classification of fishes both recent and fossil. J. W. Edwards, Ann Arbor, Mich., 517 pp. Reprint of Berg (1940) plus English translation.

Classification of genera *Brevoortia* and *Ethmidium*.

BLANC, A.

1948. Quelques observations sur la migration des Clupéidés dans le secteur de la Petite Côte (Sénégal). Bulletin des Services de l'Élevage et de Industries Animales de l'Afrique Occidentale Française, tome 1, No. 4, pp. 45–57.

General description of distribution and occurrence of *Ethmalosa dorsalis*.

BLOMEFIELD, LEONARD.

See Jenyns, 1842.

BORGSTROM, GEORG.

1961. U.S. Atlantic fisheries and current trends in supply and use. *In* Georg Borgstrom and Arthur J. Heighway, editors, Atlantic Ocean fisheries, pp. 225–255. Fishing News (Books) Ltd., London.

Menhaden fishery mentioned.

BOROUGHS, HOWARD, WALTER A. CHIPMAN, and THEODORE R. RICE.

1957. Laboratory experiments on the uptake, accumulation, and loss of radionuclides by marine organisms. *In* Report of the Committee on the effects of atomic radiation on oceanography and fisheries, pp. 80–87. National Academy of Sciences—National Research Council, Publication No. 551.

Experimental uptake of ruthenium-106 by menhaden.

BOULENGER, G. A.

1905. Poissons de la Guinée Espagnole. Memorias de la Real Sociedad Española de Historia Natural Madrid, vol. 1, No. 9, pp. 187–188.

Clupea dorsalis listed from the Rio Benito, Spanish Guinea.

BOWDICH, THOMAS EDWARD.

1825. Excursions in Madeira and Porto Santo, during the autumn of 1823, while on his third voyage to Africa . . . to which is added, by Mrs. Bowdich . . . III. Appendix: containing zoological and botanical descriptions, and translations from the Arabic. George B. Whittaker, London, 278 pp.

Original description of *Ethmalosa fimbriata* as *Clupea fimbriata*.

1826. Excursions dans les iles de Madère et de Porto. Santo, faites dans l'automne de 1823, pendant son troisième voyage en Afrique; . . . suivies . . . 3° d'un appendice contenant des observations relatives à la zoologie et à la botanique et un choix de morceaux traduits de l'arabe par Mme. Bowdich. F. G. Levrault, Paris, 447 pp.

French edition; *see* Bowdich, 1825.

BREDER, C. M., JR.

1960. Design for a fry trap. Zoologica, vol. 45, pt. 4, No. 10, pp. 155–159.

Occurrence of *Brevoortia* larvae in plastic fish trap.

1962. Effects of a hurricane on the small fishes of a shallow bay. Copeia, 1962, No. 2, pp. 459–462.

Reported occurrences of *Brevoortia patronus* larvae in fish trap catches, spring and fall, 1960.

BREUER, JOSEPH P.

1962. An ecological survey of the Lower Laguna Madre of Texas, 1953–1959. Publications of the Institute of Marine Science, Texas, vol. 8, pp. 153–183.

Reported the common occurrence of *Brevoortia gunteri* and a few *B. patronus*. Both species utilized the Arroyo Colorado for nursery grounds.

Briggs, John C.

1958. A list of Florida fishes and their distribution. Bulletin of the Florida State Museum, Biological Sciences, vol. 2, No. 8, pp. 223–318.

Brevoortia tyrannus, *B. patronus*, *B. smithi*, and *B. gunteri* listed.

Brown, Herbert H.

1948. Note on the organisation of fishery research in British West Africa. *In* Conférence de la Pêche Maritime, Dakar, 1948, pp. 279–292. Centre National d'Information Économique, Paris.

Ethmalosa fishery mentioned.

Bullis, Harvey R., Jr.

1961. A progress report on experimental fishing for sardine-like fishes in the Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute, 13th Annual Session, 1960, pp. 94–97.

Brevoortia patronus caught by midwater trawl.

Butler, Philip A. (Editor).

1959. Annotated bibliography of unpublished estuarine research in the Gulf of Mexico, 1925–1959. Gulf States Marine Fisheries Commission, New Orleans, 51 pp. (Processed).

Includes references to the distribution of marine fishes, including menhaden, in estuaries.

1960. Annotated bibliography of unpublished estuarine research in the Gulf of Mexico, supplement 1. Gulf States Marine Fisheries Commission, New Orleans, 17 pp. (Processed).

Includes references to the distribution of marine fishes, including menhaden, in estuaries.

Bychowsky, Boris E.

1957. Monogeneticheskie sosal'shchiki ikh sistema i filogenii͡a. Akademii͡a Nauk SSSR, Zoologicheskiĭ Institut Moskva, 509 pp.

Parasites of *Brevoortia gunteri* mentioned.

1961. Monogenetic trematodes, their systematics and phylogeny. English editor, William J. Hargis, Jr. American Institute of Biological Sciences, 627 pp.

English translation of Bychowsky, 1957.

Cadenat, J.

1947. Noms vernaculaires des principales formes d'animaux marins des Côtes de l'Afrique Occidentale Française. Institut Français d'Afrique Noire, Catalogue No. 2, pp. 1–56.

Ethmalosa fimbriata listed with local common names from Senegal, French Guinea, Ivory Coast, and Dahomey.

1948. Physionomie générale de la pêche maritime en A.O.F. *In* Conférence de la Pêche Maritime, Dakar, 1948. Centre National d'Information Économique, Paris. pp. 25–60.

Brief mention of *Ethmalosa* fishery.

1950. Poissons de mer du Sénégal. Institut Français d'Afrique Noire, Initiations Africaines, No. 3, 345 p.

Ethmalosa fimbriata synonym *E. dorsalis* listed with figures.

1960. Notes d'Ichtyologie ouest–africaine. XXX.—Poissons de mer ouest–africains observés du Sénégal au Cameroun et plus spécialement au large des Côtes de Sierra Leone et du Ghana. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 22, No. 4, pp. 1358–1423.

Reported occurrence of *Ethmalosa dorsalis* from Nigeria, Ghana, and Sierra Leone.

Campos Amaral, A.

1942. Contribuição ao estudo dos clupeóides das aguas brasileiras. Arquivos de Zoologia do Estado de São Paulo, vol. 3, art. 7, pp. 185–218. *Also* Revista do Museu Paulista, São Paulo, tomo 26.

Brief description of *Brevoortia tyrannus aurea* with synonymy and some references. Keys to genera and species of clupeid fishes of Brazil.

Carranza, Jorge.

1959. Pesca y recursos pesqueros. *In* Enrique Beltran, editor, Los recursos naturales del Sureste y su aprovechamiento, pp. 151–238. Instituto Mexicano de Recursos Naturales Renovables, Mexico, D.F., parte 2, tomo 3, capitulo 5.

Potential menhaden resource mentioned.

Castillo, Luis, and Zacarias Vergara.

1907. La pesca en la Bahía de Coquimba. Anales Agrónómicos, Santiago, 18 pp.

Clupea maculata mentioned.

Chabanaud, Paul, and Théodore Monod.

1926. Les poissons de Port-Étienne. Contribution à la faune ichtyologique de la région du Cap Blanc (Mauritanie française). Bulletin Comité l'Étude Histoire Scientifique de l'Afrique Occidentale Française, tome 9, No. 2, pp. 225–287.

Ethmalosa dorsalis listed.

Chipman, Walter A.

1959. The use of radioisotopes in studies of the foods and feeding activities of marine animals Pubblicazioni della Stazione Zoologica di Napoli, supplemento vol. 31, pp. 154–175.

Use of radioisotopes in food and feeding of larval and juvenile *Brevoortia tyrannus*.

1960. Biological aspects of disposal of radioactive wastes in marine environments. *In* proceedings of the Scientific Congress on the Disposal of Radioactive Wastes, Monaco, 1959, pp. 1–15. International Atomic Energy Agency, Vienna, vol. 2.

Radioactivity of *Brevoortia tyrannus* after feeding on phytoplankton cells containing ruthenium-106.

Christmas, J. Y.

1960. Greater and lesser scaup feeding on dead gulf menhaden. Auk, vol. 77, No. 3, pp. 346–347.

Observations of ducks feeding on dead *Brevoortia patronus* discarded from the shrimp trawl fishery.

Christmas, J. Y., and Gordon Gunter.

1960. Distribution of menhaden, genus *Brevoortia*, in the Gulf of Mexico. Transactions of the American Fisheries Society, vol. 89, No. 4, pp. 338–343.

Review of literature on *Brevoortia* in the Gulf of Mexico with a comparison of *B. gunteri* and *B. smithi* collected together in the northern gulf.

CHRISTMAS, J. Y., GORDON GUNTER, and EDWARD C. WHATLEY.

1960. Fishes taken in the menhaden fishery of Alabama, Mississippi, and eastern Louisiana. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 339, 10 pp.

Sampling of *Brevoortia patronus* purse seine catches for species composition.

CUSHING, D. H., FINN DEVOLD, JOHN C. MARR, and H. KRISTJONSSON.

1952. Some modern methods of fish detection. Food and Agriculture Organization of the United Nations, Fisheries Bulletin, vol. 5, Nos. 3–4, pp. 95–119.

Aerial spotting in menhaden purse seine fishery.

CUVIER, GEORGES, and ACHILLE VALENCIENNES.

1847. Histoire naturelle des poissons. P. Bertrand, Paris, tomo 20, 472 pp.

Descriptions of *Alausa aurea*, *A. tyrannus*, *A. menhaden*, *A. maculata*, and *A. caerulea*.

DARNELL, REZNEAT M.

1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publications of the Institute of Marine Science, Texas, vol. 5, pp. 353–416.

Stomachs of juvenile *Brevoortia patronus* contained phytoplankton and detritus as the principal contents.

1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. Ecology, vol. 42, No. 3, pp. 553–568.

Food of juvenile *Brevoortia patronus* and the occurrence as food of predators.

1962. Ecological history of Lake Pontchartrain, an estuarine community. American Midland Naturalist, vol. 68, No. 2, pp. 434–444.

Brevoortia patronus mentioned.

DARWIN, CHARLES R.

1842. The zoology of the voyage of H.M.S. *Beagle*, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836. Smith, Elder, and Co., London.

See Jenyns, 1842.

DE BUEN, FERNANDO.

1950. La fauna de peces del Uruguay. *In* El Mar de Solís y su fauna de peces, 2ª parte, Servicio Oceanografico y de Pesca, Publicaciones Cientificas, No. 2, pp. 45–144.

Brevoortia pectinata and *B. aurea* listed with synonymy and bibliography.

1953. Las familias de peces de importancia economica. Primer Centro Latinoamericano de Capacitación Pesquera, Oficina Regional de la FAO, Valparaiso, 311 pp.

Distribution of all species of *Brevoortia* reviewed briefly, after Hildebrand, 1948. *Brevoortia pectinata* used for bait in shark fishery, and salted or smoked for human consumption. *B. aurea* mentioned.

1958. Peces de la superfamilia Clupeoidae en aguas de Chile. Revista de Biología Marina, Valparaíso, vol. 8, Nos. 1–3, pp. 83–110.

Described *Ethmidium maculata* and *E. chilcae* as *Brevoortia* (*Ethmidium*) *maculata* and *B.* (*E.*) *chilcae*.

1959. Lampreas, tiburones, rayas y peces en la Estación de Biología Marina de Montemar, Chile. First Contribution. Revista de Biología Marina, Valparaíso, vol. 9, Nos. 1–3, pp. 1–200.

Brevoortia (*Ethmidium*) *maculata* and *B.* (*E.*) *chilcae* listed.

DE CARVALHO, VICENTE ANTÃO.

1957. Nomes vulgares de peixes Brasileiros marinhos com seus correspondentes em sistematica. Conselho coordenador do Abastecimento, Rio de Janeiro, 21 pp. (Processed.)

Brevoortia tirannus (sic), "savelha" listed.

DEEVEY, GEORGIANA BAXTER.

1956. Zooplankton. *In* Oceanography of Long Island Sound, 1952–1954, pp. 113–155. Bulletin of the Bingham Oceanographic Collection, vol. 15, pt. 5.

Filter feeding of menhaden mentioned.

DELFIN, FEDERICO T.

1900. Catálogo de los peces de Chile (continuación). Revista Chilena de Historia Natural, Ano 4, núm. 1, pp. 4–6; núm. 2, pp. 21–25.

Clupea caerulea, *C. notocanthus*, *C. maculata*, and *C. advena* listed with synonymy.

1902. Concordancia de nombres vulgares y científicos de los peces de Chile. Revista Chilena de Historia Natural, Año 6, núm. 2, pp. 71–76.

Generally the same as Delfin, 1900, with common names.

DE OLIVERA, HELENE PAES.

1942. Espécies de sardinhas que ocorrem no litoral brasileiro. Servico de Informacão Agricola Brasil, Ministerio de Agricultura, Rio de Janeiro, pp. 1–30.

A description of *Brevoortia tyrannus aurea* with figure and key to genera of Clupeidae.

DE SYLVA, DONALD P., FREDERICK A. KALBER, JR., and CARL N. SHUSTER, JR.

1962. Fishes and ecological conditions in the shore zone of the Delaware River Estuary, with notes on other species collected in deeper waters. University of Delaware Marine Laboratories, Information Series Publication No. 5, 164 pp.

Occurrence and size distribution of *Brevoortia tyrannus* in seine collections for bimonthly intervals, August 1958 to February 1960.

DEUBLER, EARL E., JR.

1958. A comparative study of the postlarvae of three flounders (*Paralichthys*) in North Carolina. Copeia, 1958, No. 2, pp. 112–116.

Diurnal variation of *Brevoortia tyrannus* postlarvae in experimental trawl catches.

DEVINCENZI, GARIBALDI J.

1920. Peces del Uruguay. Anales del Museo de Historia Natural de Montevideo, serie 2, tomo 1, entrega 4, pp. 97–138.

Review of the literature referring to *Brevoortia* in the region.

1924. Peces del Uruguay (Conclusion). Anales del Museo de Historia Natural de Montevideo, serie 2, tomo 1, entrega 5, pp. 139–293.

Clupea pectinata Jenyns reported as *Brevoortia tyrannus* with counts and body proportions for nine specimens.

1925. El primer ensayo sobre ictiología del Uruguay. La clase "Peces" de la zoología de don Dámaso A. Larrañaga. Anales del Museo de Historia Natural de Montevideo, serie 2, tomo 1, entrega 6, pp. 295–323.

Clupea laccia vel 20–radiata described as *Brevoortia tyrannus.*

Devincenzi, Garibaldi J., and Luis P. Barattini.

1928. Álbum ictiológico del Uruguay. Anales del Museo de Historia Natural de Montevideo, serie 2, tomo 2, entrega 4, 24 plates.

A drawing of *Brevoortia tyrannus.*

Dollo, Louis.

1904. Poissons. Expédition Antarctique Belge. Résultats du Voyage du S.Y. *Belgica,* Zoologie, pt. 4, 239 pp.

Potamalosa notacanthus reported from South America.

Doutre, M. P.

1959. Composition chimique du poisson. Variations annuelles de la teneur en matières grasses de trois clupéidés du Senegal (*Ethmalosa fimbriata* Bowdich, *Sardinella eba* C.V., *Sardinella aurita* C.V.). Communications de la Section Technique des Pêches Maritimes, Dakar, No. 124, 4 pp.

Average body fat contents by month.

Dumeril, Auguste.

1861. Reptile et poissons de l'Afrique Occidentale . . . Archives du Muséum d'Histoire Naturelle, Paris, 1858–61, vol. 10, pp. 137–160, 233–240, 261–264.

Clupea aurea from Senegal.

Edwards, Henri Milne.

See Milne–Edwards, 1840.

Ellison, William A., Jr.

1951. The menhaden. *In* Survey of marine fisheries of North Carolina. Harden F. Taylor and associates: pp. 85–107. University of North Carolina Press, Chapel Hill, N.C.

General account of menhaden and the menhaden purse seine fishery.

Evermann, Barton Warren, and William Converse Kendall.

1906. Notes on a collection of fishes from Argentina, South America, with descriptions of three new species. Proceedings of the U.S. National Museum, vol. 31, No. 1482, pp. 67–108.

Brevoortia specimens not distinguished from *B. tyrannus.*

Fowler, Henry W.

1911. Notes on clupeoid fishes. Proceedings of the Academy of Natural Sciences, Philadelphia, vol. 63, pp. 204–221.

Reported occurrence of *Brevoortia tyrannus* along the Atlantic Coast of the U.S., *B. tyrannus patronus* from the Gulf of Mexico, *B. tyrannus aurea* from Brazil, and *B. tyrannus dorsalis* from Gaboon River, West Africa.

1936. The marine fishes of West Africa based on the collection of the American Museum Congo Expedition, 1909–1915. Bulletin of the American Museum of Natural History, New York, vol. 70, pt. 1, pp. 1–605.

Brevoortia tyrannus reported from Senegal, description of specimens from United States. *Ethmalosa fimbriata* described with extensive synonymy and some references not included in this bibliography.

1940. Fishes obtained by the Wilkes Expedition, 1838–1842. Proceedings of the American Philosophical Society, vol. 82, No. 5, pp. 733–800.

Brevoortia pectinata listed with figure. *Ethmidium maculatum* listed with figure.

1942. A list of the fishes known from the coast of Brazil. Arquivos de Zoologia do Estado de São Paulo, vol. 3, art. 6, pp. 115–184. *Also* Revista do Museu Paulista, São Paulo, tomo 26.

Brevoortia tyrannus with synonymy for *B. aurea* and *B. pectinata* listed. A figure of *B. tyrannus aurea.*

1944. Fishes of Chile. Systematic catalog. Pt. 2. Revista Chilena de Historia Natural Pura y Aplicada. Años 46–47, pp. 15–116.

Ethmidium maculatum listed with synonymy.

1945. Los peces del Peru. Catálogo Sistemático de los peces que habitan en aguas peruanas. Museo de Historia Natural "Javier Prado" Universidad Nacional Mayor de San Marcos, Lima, 298 pp.

Ethmidium maculatum listed with synonymy.

1948. Os peixes de água doce do Brasil. Arquivos de Zoologia do Estado de São Paulo, vol. 6, pt. 1, pp. 1–204.

Original description of new subfamily Brevoortinae. *Brevoortia aurea* listed.

1951a. Analysis of the fishes of Chile. Revista Chilena de Historia Natural Pura y Aplicada, Años 51–53, pp. 263–326.

Ethmidium maculatum placed in subfamily Brevoortinae.

1951b. The Brazilian and Patagonian fishes of the Wilkes Expedition, 1838–1842. Boletim do Instituto Paulista de Oceanografia, São Paulo, tomo 2, fasc. 1, pp. 1–39.

Brevoortia pectinata listed and compared with *B. tyrannus.*

Gay, Claudio.

1848. Peces de Guichinot. *In* Historia física y política de Chile. . . . Zoologia, tomo 2, pp. 137–370. Paris.

Alosa maculata and *A. caerulea* listed.

Gill, Theodore.

1861. Synopsis of the subfamily Clupeinae, with descriptions of new genera. Proceedings of the

Academy of Natural Sciences, Philadelphia, vol. 13, pp. 33–38.

Original description of genus *Brevoortia*.

Goode, G. Brown.

1878. A revision of the American species of the genus *Brevoortia*, with a description of a new species from the Gulf of Mexico. Proceedings of the U.S. National Museum, vol. 1, pp. 30–42.

Original descriptions of *Brevoortia patronus* and *B. tyrannus brevicaudata* including remarks about *B. pectinata* and *B. aurea*.

1879. The natural and economical history of the American menhaden. Report of the U.S. Commission of Fish and Fisheries, 1877, app. A, 529 pp.

An extensive review of the biology, fishery, and industry for the Atlantic menhaden, *Brevoortia tyrannus*. Also included are summary remarks about *B. patronus*, *B. aurea*, and *B. pectinata*.

Gordon, Bernard L.

1961. A guide book to the marine fishes of Rhode Island. Book & Tackle Shop, Watch Hill, R.I., 136 pp.

Brief description and general account of *Brevoortia tyrannus*.

Grant, George C.

1962. Predation of bluefish on young Atlantic menhaden in Indian River, Delaware. Chesapeake Science, vol. 3, No. 1, pp. 45–47.

Stomach content analysis of young bluefish showed juvenile menhaden to be one of the more important foods.

Gras, Roger.

1961. Liste des poissons du Bas-Dahomey faisant partie de la collection du laboratoire d'hydrobiologie du service des eaux, forets, et chasses du Dahomey. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 23, No. 2, pp. 572–586.

Ethmalosa fimbriata listed as abundant.

Guichenot.

1848. *See* Gay, Claudio, 1848.

Gunter, Gordon.

1957. Predominance of the young among marine fishes found in fresh water. Copeia, 1957, No. 1, pp. 13–16.

Brevoortia tyrannus mentioned after Massmann, 1954.

1958. Population studies of the shallow water fishes of an outer beach in south Texas. Publications of the Institute of Marine Science, Texas, vol. 5, pp. 186–193.

Brevoortia sp. occurred on the outer beach April–August, 1949.

1961. Some relations of estuarine organisms to salinity. Limnology and Oceanography, vol. 6, No. 2, pp. 182–190.

Relation of haul seine catches of *Brevoortia patronus* to low salinity.

Gunter, Gordon, and J. Y. Christmas.

1960. A review of literature on menhaden, *Brevoortia patronus* Goode. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 363, 31 pp.

Gunter, Gordon, and William J. Demoran.

1961. Lateral lines and an undescribed sensory area on the head of the gulf menhaden, *Brevoortia patronus*. Copeia, 1961, No. 1, pp. 39–42.

Description of the cephalic sensory canals and review of the literature of the structure in other fishes.

Gunter, Gordon, and William E. Shell, Jr.

1958. A study of an estuarine area with water-level control in the Louisiana marsh. Proceedings of the Louisiana Academy of Science, vol. 21, pp. 5–34.

Monthly catches of *Brevoortia patronus*, 1951–53, with the relation of haul seine catches to low salinity.

Günther, Albert.

1868. Catalogue of the fishes in the British Museum. Taylor and Francis, London, vol. 7, 512 pp.

Clupea menhaden, *C. aurea*, *C. pectinata*, and *C. dorsalis* listed and briefly described.

Halkett, Andrew.

1913. Check list of the fishes of the Dominion of Canada and Newfoundland. C. H. Parmelee, Ottawa, 138 pp.

Brevoortia tyrannus listed.

Hall, F. G., and F. H. McCutcheon.

1938. The affinity of hemoglobin for oxygen in marine fishes. Journal of Cellular and Comparative Physiology, vol. 11, No. 2, pp. 205–212.

Affinity of hemoglobin of *Brevoortia tyrannus* for oxygen in buffered solutions at different hydrogen ion concentrations.

Harder, Wilhelm.

1958. Zur Anatomie des Darmtraktes einiger Familien der Clupeoidea: Clupeidae, Dorosomatidae, Dussumieriidae und Engraulididae (Clupeiformes, Pisces). Kurze Mitteilungen aus dem Institut für Fischereibiologie der Universität Hamburg, Nr. 8, Dezember, pp. 11–61.

Descriptions and drawings of the digestive tracts of juvenile *Brevoortia tyrannus* and *B. patronus*.

1960. Vergleichende Untersuchungen zur Morphologie des Darmes bei Clupeoidea. Zeitschrift für wissenschaftliche Zoologie, Band 163, Heft 1½, pp. 65–167.

Brevoortia tyrannus mentioned.

Hargis, William J., Jr.

1959. Systematic notes on the monogenetic trematodes. Proceedings of the Helminthological Society of Washington, vol. 26, No. 1, pp. 14–31.

Parasites of *Brevoortia patronus* and *B. gunteri* mentioned.

1961. *See* Bychowsky, 1961.

Haskell, Winthrop A.

1961. Gulf of Mexico trawl fishery for industrial species. Commercial Fisheries Review, vol. 23, No. 2, pp. 1–6. Also Separate No. 612, 6 pp.

Monthly occurrence of three species, listed as

Brevoortia spp., in the otter trawl landings of industrial fish during 1959.

Hedgpeth, Joel W.

1957. II. Biological aspects. Treatise on marine ecology and paleoecology (Joel W. Hedgpeth, editor). Geological Society of America, Memoir 67, vol. 1, ch. 23, Estuaries and lagoons, pp. 693–749.

Distribution of *Brevoortia tyrannus* and *B. gunteri* in relation to salinity.

Hellier, Thomas R., Jr.

1962. Fish production and biomass studies in relation to photosynthesis in the Laguna Madre of Texas. Publications of the Institute of Marine Science, Texas, vol. 8, pp. 1–22.

Brevoortia patronus and *B. gunteri* listed.

Herman, Sidney S.

1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnology and Oceanography, vol. 8, No. 1, pp. 103–109.

Monthly occurrences of *Brevoortia tyrannus* eggs and larvae.

Herrington, William C., and Robert A. Nesbit.

1943. Fishery management. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report No. 18, 69 pp.

Mention of the exaggeration of estimated numbers of menhaden.

Hildebrand, Henry H.

1958. Estudio biologicos preliminares sobre la Laguna Madre de Tamaulipas. Ciencia, Mexico, vol. 17, Nos. 7–9, pp. 151–173.

Brevoortia gunteri reported as rare in beach seine catches.

Hildebrand, Samuel F.

1946. A descriptive catalog of the shore fishes of Peru. Bulletin of the U.S. National Museum, No. 189, 530 pp.

Original description of *Ethmidium chilcae.*

1948. A review of the American menhaden, genus *Brevoortia,* with a description of a new species. U.S. National Museum, Smithsonian Institution, Miscellaneous Collection, vol. 107, No. 18, pp. 1–39.

Comparison and summary review of the seven species of menhaden occurring along the Atlantic coasts of North and South America: *Brevoortia tyrannus, B. patronus, B. brevicaudata, B. pectinata, B. aurea, B. smithi,* and *B. gunteri.*

Hoese, Hinton D.

1958. A partially annotated checklist of the marine fishes of Texas. Publications of the Institute of Marine Science, Texas, vol. 5, pp. 312–352.

Brevoortia patronus and *B. gunteri* listed.

Hornell, James.

1928. Report on the fishery resources of Sierra Leone. Government Printing Office, Freetown, 51 pp.

Brief account of the fishery for *Ethmalosa fimbriata.*

Hubbs, Clark.

1958. A check–list of Texas freshwater fishes. Texas Game and Fish Commission, Inland Fisheries Series, No. 3, 14 pp.

Reported *Brevoortia gunteri* from fresh water.

Hyrtl, Joseph.

1855. Über die accessorischen Kiemenorgane der Clupeaceen, nebst Bemerkungen über den Darmcanal derselben. Denkschriften Koeniglige Akademie der Wissenschaften, Vienna, Band 10, pp. 47–57.

Branchiostegals of *Clupanodon aureus* (*B. aurea*) and *Alausa tyrannus* (*B. tyrannus*).

Ihering, H. von

1897. Os peixes da costa do mar no Estado do Rio Grande do Sul. Revista do Museu Paulista, São Paulo, vol. 2, pp. 25–63.

Brevoortia tyrannus "savelha" mentioned briefly. Species used principally for agricultural fertilizer.

Irvine, Frederick Robert.

1947. The fishes and fisheries of the Gold Coast. Crown Agents, London, 352 pp.

General description of *Ethmalosa dorsalis.*

Jenyns, Leonard.

1842. The fishes. *In* Charles R. Darwin, editor, The zoology of the voyage of H.M.S. *Beagle,* under the command of Captain Fitzroy, R.N., during the years 1832 to 1836, pt. 4, pp. 1–169. Smith, Elder, and Co., London.

Original description of *Alosa pectinata.*

Johnson, Malcolm C.

1954. Preliminary experiment on fish culture in brackish–water ponds. Progressive Fish-Culturist, vol. 16, No. 3, pp. 131–133.

Occurrence of menhaden in brackish water pond mentioned.

Joseph, Edwin B., and Ralph W. Yerger.

1956. The fishes of Alligator Harbor, Florida, with notes on their natural history. Florida State University Studies No. 22, pp. 111–156.

Brevoortia patronus listed.

June, Fred C.

1958. Variation in meristic characters of young Atlantic menhaden, *Brevoortia tyrannus.* Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-verbaux des Réunions, vol. 143, pt. 2, pp. 26–35.

Two populations of menhaden along the Atlantic coast of the United States, indicated from meristic differences of juveniles.

1961a. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1957; with a brief review of the commercial fishery. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 373, 39 pp.

A detailed review of the catch composition and the fishery with appendix tables of age, sex, weight, and length, by geographic areas with summary analyses of the data.

1961b. The menhaden fishery of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Leaflet No. 521, 13 pp. [Processed.]

Brief review of the fishery and life history of *Brevoortia tyrannus.*

June, Fred C., and J. Lockwood Chamberlin.

1959. The role of the estuary in the life history and biology of Atlantic menhaden. Proceedings of the Gulf and Caribbean Fisheries Institute, 11th Annual Session, 1958, pp. 41–45.

Observations on the entry of larval *Brevoortia tyrannus* and their development and distribution in the estuarine nursery grounds.

June, Fred C., and William R. Nicholson.

1964. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1958; with a brief review of the commercial fishery. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 446, 40 pp.

A detailed review of the catch composition and the fishery with appendix tables of age, sex, weight, and length, by geographic areas with summary analyses of the data.

June, Fred C., and John W. Reintjes.

1959. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1952–55; with a brief review of the commercial fishery. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 317, 65 pp.

A detailed review of the catch composition and the fishery with appendix tables of age, sex, weight, and length, by geographic areas with summary analyses of the data.

1960. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1956; with a brief review of the commercial fishery. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 336, 38 pp.

A detailed review of the catch composition and the fishery with appendix tables of age, sex, weight, and length, by geographic areas with summary analyses of the data.

June, Fred C., and Charles M. Roithmayr.

1960. Determining age of Atlantic menhaden from their scales. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin No. 171, vol. 60, pp. 323–342.

Methods and results of determining age of *Brevoortia tyrannus* by viewing scales.

Kner, Rudolf, and Franz Steindachner.

1866. Neue Fische aus dem Museum der Herren Joh. Ces. Godeffroy and Sohn in Hamburg. Sitzungsberichte der Mathematisch - Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften, Vienna, Band 54, Heft 1, pp. 356–395.

Original description of *Alausa fimbriata* of Valparaiso (sic) similar to *A. pectinata* Jenyns.

Kuntz, Albert, and Lewis Radcliffe.

1917. Notes on the embryology and larval development of twelve teleostean fishes. Bulletin of the U.S. Bureau of Fisheries, vol. 35, pp. 88–134.

Description of eggs and larvae of *Brevoortia tyrannus*.

Lagler, Karl F., John E. Bardach, and Robert R. Miller.

1962. Ichthyology. John Wiley and Sons, New York, 545 pp.

Filter feeding rate and body fat content of *Brevoortia tyrannus* mentioned. Brief mention of general migration and gill area of *Brevoortia*.

Larrañaga, Dámaso Antonio.

1923. Escritos . . . Revista del Instituto Histórico y Geográfico del Uruguay, Montevideo, tomo 2, pp. 5–512.

Clupea 20-radiata synonym for *Brevoortia pectinata*.

Leach, W. E.

1818. Cymothoadées. Dictionnaire des Sciences Naturelles, Paris, tome 12, pp. 338–354.

Parasitic isopod in branchial chamber of menhaden.

Leim, A. H., and L. R. Day.

1959. Records of uncommon and unusual fishes from eastern Canadian waters, 1950–1958. Journal of the Fisheries Research Board of Canada, Vol. 16, No. 4, pp. 503–514.

Juvenile and adult *Brevoortia tyrannus* reported from New Brunswick.

Longhurst, Alan R.

1957. The food of the demersal fish of a West African estuary. Journal of Animal Ecology, vol. 26, No. 2, pp. 369–387.

Ethmalosa reported as food of guitarfish, *Rhinobatus rasus;* catfish, *Arius latiscutatus;* and shine-nose, *Galeoides decadactylus.*

1960a. Fish landings in Sierra Leone during 1959. Fisheries Development and Research Unit, Freetown, Occasional Paper No. 1 (unpaged).

A brief review of the fishery and landings of *Ethmalosa dorsalis.*

1960b. Local movements of *Ethmalosa fimbriata* off Sierra Leone from tagging data. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 22, No. 4, pp. 1337–1340.

Recovery of 24 of 2,012 tagged *Ethmalosa fimbriata* showed movement northward from Freetown.

1961. Report on the fisheries of Nigeria, 1961. Federal Fisheries Service, Ministry of Economic Development, Lagos, 42 pp. (processed).

Distribution and fishery for *Ethmalosa* reviewed briefly.

Lozano-Rey, Luis.

1950. Etude systématique des Clupéides et des Engraulidés de l'Espagne, du Maroc et du Sahara Espagnols. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-verbaux des Réunions, vol. 126, pp. 7–20.

Brief description and synonymy of *Ethmalosa fimbriata.*

Lunz, G. Robert.

1956. Harvest from an experimental one-acre salt-water pond at Bears Bluff Laboratories, South Carolina. Progressive Fish-Culturist, vol. 18, No. 2, pp. 92–94.

Percentage occurrence of *Brevoortia* by number and weight in a salt water pond.

Mainguy, P., and M. Doutre.

1958. Variations annuelles de la teneur en matières grasses de trois Clupéidés du Sénégal. Revue des Travaux. Institut Scientifique et Technique des Pêches Maritimes, Paris, tome 22, fasc. 3, pp. 303–321.

Annual variations in body fat content of *Ethmalosa fimbriata.*

Mairs, Donald F., and Carl J. Sindermann.

1962. A serological comparison of five species of Atlantic clupeoid fishes. The Biological Bulletin, vol. 123, No. 2, pp. 331–343.

Brevoortia tyrannus compared with *Alosa sapidissima, A. aestivalis, A. pseudoharengus,* and *Clupea harengus.*

Mann F., Guillermo.

1950. Peces de Chile. Clave de determinación de las especies importantes. Instituto Investigaciones Veterinarias, Ministero de Agricultura, Santiago, 44 pp., 89 figs.

Ethmidium maculatum and *E. chilcae* in a key to fishes of commercial importance.

1954. Vida de los peces en aguas chilenas. Instituto Investigaciones Veterinarias, Ministero de Agricultura, Santiago, 342 pp.

A description of *Ethmidium maculatum maculatum* and *E. m. chilcae* with brief notes on biology.

Mansueti, Romeo J.

1962. Distribution of small, newly metamorphosed sea lampreys, *Petromyzon marinus*, and their parasitism on menhaden, *Brevoortia tyrannus*, in mid-Chesapeake Bay during winter months. Chesapeake Science, vol. 3, No. 2, pp. 137–139.

Reported occurrence of sea lampreys attached to Atlantic menhaden in the Chesapeake Bay.

Marak, Robert R., and John B. Colton, Jr.

1961. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1953. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 398, 61 pp.

One *Brevoortia tyrannus* egg collected at the surface with 1-meter plankton net, 10 miles S.W. of Martha's Vineyard on June 3, 1953.

Marak, Robert R., John B. Colton, Jr., and Donald B. Foster.

1962. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1955. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 411, 66 pp.

Twelve *Brevoortia tyrannus* eggs collected at the surface with Hardy plankton sampler, 75 miles south of Nantucket on May 16, 1955.

Marak, Robert R., John B. Colton, Jr., Donald B. Foster, and David Miller.

1962. Distribution of fish eggs and larvae, temperature and salinity in the Georges Bank-Gulf of Maine area, 1956. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 412, 95 pp.

Three *Brevoortia tyrannus* larvae (4.5–8.2 mm.) collected in a 1-meter plankton net on the surface off Woods Hole, Mass., on June 24, 1956.

Marvin, Kenneth T., and Larence M. Lansford.

1962. Phosphorus content of some fishes and shrimp in the Gulf of Mexico. Publications of the Institute of Marine Science, Texas, vol. 8, pp. 143–146.

Percent of phosphorus by weight for two lots of *Brevoortia patronus.*

Massmann, William H.

1954. Marine fishes in fresh and brackish waters of Virginia rivers. Ecology, vol. 35, No. 1, pp. 75–78.

Occurrence of *Brevoortia tyrannus* in fresh water.

1961. Fishes and fish larvae collected from Atlantic plankton cruises of R/V *Pathfinder*, December 1959–December 1960. Institute of Marine Science, Virginia Fisheries Laboratory, Special Scientific Report No. 26, 3 pp. (Processed.)

Monthly occurrence of *Brevoortia tyrannus* larvae in plankton collections with size range in millimeters.

Massmann, William H., John J. Norcross, and Edwin B. Joseph.

1962. Atlantic menhaden larvae in Virginia coastal waters. Chesapeake Science, vol. 3, No. 1, pp. 42–45.

Occurrence of larval *Brevoortia tyrannus* in plankton collections from the Atlantic Ocean off the mouth of Chesapeake Bay from November to April, 1959–60.

McAllister, D. E.

1960. List of the marine fishes of Canada. National Museum of Canada, Bulletin No. 168, Biological Series, No. 62, 76 pp.

Brevoortia tyrannus listed from the Atlantic Ocean.

McHugh, J. L.

1960. The pound-net fishery in Virginia. Pt. 2—Species composition of landings reported as menhaden. Commercial Fisheries Review, vol. 22, No. 2, pp. 1–16. *Also* Separate No. 518, 16 pp.

Semi-monthly landings of *Brevoortia tyrannus* and associated species from pound nets.

McHugh, J. L., R. T. Oglesby, and A. L. Pacheco.

1959. Length, weight, and age composition of the menhaden catch in Virginia waters. Limnology and Oceanography, vol. 4, No. 2, pp. 145–162.

Aspects of biology and life history of *Brevoortia tyrannus* from pound net and purse seine catches in Chesapeake Bay.

Merriman, Daniel, and Ruth C. Sclar.

1952. The pelagic fish eggs and larvae of Block Island Sound. *In* Hydrographic and biological studies of Block Island Sound, pp. 165–219. Bulletin of the Bingham Oceanographic Collection, vol. 13, art. 3.

Absence of menhaden eggs and larvae noted from monthly plankton collections, 1943–46.

Migdalski, Edward C.

1958. Angler's guide to the salt water game fishes. Ronald Press, New York, 506 pp.

A popular account listing Atlantic menhaden as food of swordfish, tuna, Atlantic bonito, cobia, gray weakfish, spotted weakfish, channel bass, black drum, and striped bass.

Milne-Edwards, Henri.

1840. Histoire naturelle des Crustacés. Paris, tome 3, 605 pp.

Parasitic isopods in *Brevoortia tyrannus*.

Monod, Théodore.

1927. Contribution à l'étude de la faune du Cameroun. I. Pisces. Faune des colonies françaises, tome I, pp. 643–742.

Young *Ethmalosa dorsalis* from the stomach contents of several demersal fishes. Figure of gills and stomach ("gizzard").

1949. Sur l'appareil branchiospinal de quelques Téléostéens tropicaux. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 11, Nos. 1–2, pp. 36–76.

Ethmalosa fimbriata branchial apparatus and pharynx described and figured.

1961. *Brevoortia* Gill 1861 et *Ethmalosa* Regan 1917. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 23, No. 2, pp. 506–547.

Comparison of the genera including scales, dermal head structure, intestinal tract, branchial apparatus, and vertebral column. Conclusion: Similar but distinct genera.

Moody, Harold L.

1961. Exploited fish populations of the St. Johns River, Florida. Quarterly Journal of the Florida Academy of Sciences, vol. 24, No. 1, pp. 1–18.

Brevoortia smithi reported from the St. Johns River.

Nicol, J. A. Colin.

1960. The biology of marine animals. Interscience Publishers, Inc., New York, 707 pp.

Brevoortia gill area and scale composition mentioned.

Oliver Schneider, Carlos.

1943. Catalogo de los peces marinos del litoral de Concepción y Arauco. Boletín de la Sociedad de Biología de Concepción, tomo 17, pp. 75–126.

Clupea maculata listed.

Osorio, Balthazar.

1905. Indiçãcoes de algumas especies que devem ser accrescentados á fauna ichthyologica da ilha de S. Thomé. Jornal de Sciencias Mathematicas, Physicas e Naturaes, Lisbon, vol. 7, No. 27, pp. 156–158.

Clupea dorsalis listed.

Otorubio, Fubara O.

1959. Fisheries development in Nigeria with special reference to the Western Region. Fishermen's Bulletin, Haifa, No. 20, pp. 31–32.

Ethmalosa fimbriata mentioned.

Pearcy, William G., and Sarah W. Richards.

1962. Distribution and ecology of fishes of the Mystic River Estuary, Connecticut. Ecology, vol. 43, No. 2, pp. 248–259.

Two *Brevoortia tyrannus* larvae in collections from June and July.

Peck, James I.

1894. On the food of menhaden. Bulletin of the U.S. Fish Commission, vol. 13, pp. 113–126.

A detailed account of the food organisms found in *Brevoortia tyrannus* and a description of the gill arrangement for filtering organisms, principally phytoplankton, from the water.

Pérez Canto, C.

1912. La fauna ictiológica de Chile considerada como requeza nacional. Santiago, pp. 3–45.

Clupea maculata and *C. notocanthus* listed.

Perlmutter, Alfred.

1959. Changes in the populations of fishes and in their fisheries in the middle Atlantic and Chesapeake regions, 1930–1955. Transactions of the New York Academy of Science, series 2, vol. 21, No. 6, pp. 484–496.

Menhaden fishery briefly mentioned.

1961. Guide to marine fishes. New York University Press, New York, 431 pp.

Brief general description and key to *Brevoortia tyrannus*.

Perugia, Alberto.

1891. Appunti sopra alcuni pesci sud-americani conservatinel Museo Civico di Storia Naturale dí Genóva. Annali del Museo Civico di Storia Naturale dí Genóva, 1890–1891, serie 2, vol. 10, No. 30, pp. 605–657.

Reports *Clupea aurea* from La Plata River.

Porter, Cárlos E.

1909a. Breve nota de ictiologia—Enumeración de las especies más importantes comunes á Chile y al Perú. Revista Universitaria, Organo de la Universidad Mayor de San Marcos, Lima, Año 3, pp. 1–14.

Clupea notocanthus listed.

1909b. Ictiología. Enumeración de especies importantes comunes a las aguas de Chile y de Perú. Revista Chilena de Historia Natural. Ãno 13, núms. 4–5, pp. 280–293.

Cupea (sic) *notocanthus* listed.

Postel, E.

1950. Note sur *Ethmalosa fimbriata* (Bowdich). Bulletin des Services de l'Élevage et des Industries Animales de l'Afrique Occidentale Française, tome 3, No. 1, pp. 49–59.

Distribution, occurrence, life history, and fishery for *Ethmalosa fimbriata*.

1959. Liste commentée des poissons signalés dans l'Atlantique tropico-oriental nord, du cap Spartel au cap Roxo, suivie d'un bref aperçu sur leur répartition bathymétrique et geógraphique. Bulletin de la Société Scientifique de Bretagne, tome 34, fasc. 1–2, pp. 129–170.

Brevoortia tyrannus and *Ethmalosa fimbriata* listed.

PRICE, EMMETT W.

1961. North American monogenetic trematodes. IX. The families Mazocraeidae and Plectanocotylidae. Proceedings of the Biological Society of Washington, vol. 74, pp. 127–155.

Parasites of *Brevoortia patronus*, *B. gunteri* and *B. tyrannus*.

QUIJADA B., BERNARDINO.

1913. Catálogo ilustrado i descriptivo de los peces chilenos i extranjeros conservados en el museo nacional. Boletín del Museo Nacional de Chile, tomo 5, nùm. 1, Santiago, pp. 7–128.

Clupea maculatus and *C. advena* listed.

REED, EDWYN C.

1897. Catálogo de los peces chilenos. Anales Universidad de Chile, tomo 98, pp. 653–673. *Also* printed separately, pp. 3–24.

Clupea caerulea, *C. maculata*, *C. notocanthus*, and *C. pectinata* (not Jenyns) listed.

REGAN, C. TATE.

1915. A collection of fishes from Lagos. Annals and Magazine of Natural History, London, series 8, vol. 15, No. 85, pp. 124–130.

Clupea dorsalis mentioned.

1917. A revision of the clupeoid fishes of the genera *Pomolobus*, *Brevoortia*, and *Dorosoma*, and their allies. Annals and Magazine of Natural History, series 8, vol. 19, No. 112, pp. 297–316.

Brief description and synonymy of *Brevoortia tyrannus*, *B. pectinata*, and *Ethmidium maculatum*.

A new genus, *Ethmalosa* for *Alausa dorsalis* Valenciennes (1847).

REINTJES, JOHN W.

1960. Continuous distribution of menhaden along the South Atlantic and gulf coasts of the United States. Proceedings of the Gulf and Caribbean Fisheries Institute, 12th Annual Session, 1959, pp. 31–35.

A brief review of the distribution of the North American menhadens, with some evidence of greater abundance in southern Florida waters than reported previously.

1961. Menhaden eggs and larvae from M/V *Theodore N. Gill* cruises, South Atlantic coast of the United States, 1953–54. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 393, 7 pp.

Brevoortia species eggs and larvae collected during three winter cruises but not during six cruises from April to November.

1962. Development of eggs and yolk-sac larvae of yellowfin menhaden. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin 202, vol. 62, pp. 93–102.

Descriptions and illustrations of artificially fertilized eggs and resulting yolk-sac larvae of *Brevoortia smithi*.

REINTJES, JOHN W., JAMES Y. CHRISTMAS, JR., and RICHARD A. COLLINS.

1960. Annotated bibliography on biology of American menhaden. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin 170, vol. 60, pp. 297–322.

Bibliography of genus *Brevoortia* in publications before and during 1957. Some very brief annotations and a subject index are included.

REINTJES, JOHN W., and FRED C. JUNE.

1961. A challenge to the fish meal and oil industry in the Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute, 13th Annual Session, 1960, pp. 62–66.

Some observations on the distribution and abundance of menhaden and other clupeoid fishes in the Gulf of Mexico, with suggestions for exploration.

REINTJES, JOHN W., and CHARLES M. ROITHMAYR.

1960. Survey of the ocean fisheries off Delaware Bay, supplement report, 1954–57. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 347, 18 pp.

Menhaden purse seine fishery mentioned but excluded from the report.

RENFRO, WILLIAM C.

1960. Salinity relations of some fishes in the Aransas River, Texas. Tulane Studies in Zoology, vol. 8, No. 3, pp. 83–91.

Occurrence of juvenile *Brevoortia patronus* in salinity of 54.3°/oo and larvae from 0.5 and 47.6°/oo

RICHARDS, SARAH W.

1959. Pelagic fish eggs and larvae of Long Island Sound. *In* Oceanography of Long Island Sound. Bulletin of the Bingham Oceanographic Collection, vol. 17, art. 1, pt. 6, pp. 95–124.

Occurrence of eggs and larvae of *Brevoortia tyrannus* from May to October, 1954–55.

1963a. The demersal fish population of Long Island Sound. I. Species composition and relative abundance in two localities, 1956–57. Bulletin of the Bingham Oceanographic Collection, vol. 18, art. 2, pp. 5–31.

Twenty-nine *Brevoortia tyrannus* collected with experimental shrimp trawl in November, December, January, February, and June. Size ranged from 16 to 305 mm.

1963b. The demersal fish population of Long Island Sound. II. Food of the juveniles from a sand-shell locality (Station I). Bulletin of the Bingham Oceanographic Collection, vol. 18, art. 2, pp. 32–72.

Stomach contents of 28 juvenile and yearling *Brevoortia tyrannus* were primarily crustaceans with *Balanus* nauplii and cyprids, and *Neomysis americanus* constituting the bulk of the food. Difference noted from Peck

(1894) who described phytoplankton the primary summer diet.

1963c. The demersal fish population of Long Island Sound. III. Food of the juveniles from a mud locality (Station 3A). Bulletin of the Bingham Oceanographic Collection, vol. 18, art. 2, pp. 73–101.

One *Brevoortia tyrannus* (100 mm.) contained *Acartia* spp., *Anchoa mitchilli* larvae, and *Labidocera aestiva*.

Richmond, E. Avery.

1962. The fauna and flora of Horn Island, Mississippi. Gulf Coast Research Laboratory, Ocean Springs, Miss., Gulf Research Reports, vol. 1, No. 1, pp. 59–106.

Reported the occurrence of *Brevoortia patronus*.

Robas, John S.

1959. Menhaden purse seining. *In* H. Kristjonsson, editor, Modern fishing gear of the world, pp. 394–399. Fishing News (Books) Ltd., London.

Description of menhaden purse seine fishing with an account of modern development.

Rochebrune, Alphonse Trémeau de

1883. Poissons. *In* Octave Doin, editor, Faune de la Sénégambie, Paris, pp. 1–166 and 6 plates in the Atlas volume.

Clupea aurea listed. Confirmed Dumeril, 1861.

Roithmayr, Charles M.

1963. Distribution of fishing by purse seine vessels for Atlantic menhaden, 1955–1959. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 434, 22 pp.

Monthly distribution of purse seine sets along the Atlantic coast of the U.S., for a 5-year period. Information obtained from logbooks kept by vessel personnel.

Rosen, Albert.

1959. Summary of Florida commercial marine landings, and an analysis of the catch and effort of certain species, 1958. University of Miami, Marine Laboratory, Publication No. 59–4, 55 p.

Landings of menhaden in Florida by county.

1960. Summary of Florida commercial marine landings, 1959, and an analysis of the catch and effort of certain species. University of Miami, Marine Laboratory, Publication No. 60–2, 53 pp.

Landings of menhaden in Florida by county.

Rosen, Albert, and Richard K. Robinson.

1961. Summary of Florida commercial marine landings, 1960, and an analysis of the catch and effort of certain species. University of Miami, Institute of Marine Science, No. 61–2, 32 pp.

Landings of menhaden in Florida by county.

1962a. Summary of Florida commercial marine landings, 1961. University of Miami, Institute of Marine Science, No. 62–5, 20 pp.

Landings of menhaden in Florida by county.

1962b. Summary of Florida commercial marine landings, 1961, and an analysis of the catch and effort of certain species. University of Miami, Institute of Marine Science, No. 62–7, 32 pp.

Landings of menhaden in Florida by county.

Salzen, E. A.

1958. Observations on the biology of the West African shad, *Ethmalosa fimbriata* (Bowdich). Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 20, No. 4, pp. 1388–1426.

A detailed account of the fishery and life history including size, weight, and sexual maturity from catches in the Sierra Leone River Estuary.

Santos, Eurico.

1952. Nossos peixes marinhos. F. Griguit e Cia., Rio de Janeiro, 265 pp.

Brevoortia tyrannus aurea "savelha" mentioned.

Schwartz, Frank J.

1961. Fishes of Chincoteague and Sinepuxent Bays. American Midland Naturalist, vol. 65, No. 2, pp. 384–408.

Occurrence of juvenile *Brevoortia tyrannus* during June and July.

Shuster, Carl N., Jr.

1959. A biological evaluation of the Delaware River Estuary. University of Delaware, Marine Laboratories, Information Series, Publication No. 3, 77 pp.

Fishery for *Brevoortia tyrannus* reviewed briefly.

Silva, R. D.

1944. Nomes vulgares de peixes encontrados no entreposto de pesca do Rio de Janeiro, com seus correspondentes em sistematica. Servico de Informacão Agricola Brasil, Ministerio de Agricultura, Rio de Janeiro, Boletim, vol. 33, No. 9, pp. 57–66.

Brevoortia "savelha" listed.

Simmons, Ernest G.

1957. An ecological survey of the upper Laguna Madre of Texas. Publications of the Institute of Marine Science, Texas, vol. 4, No. 2, pp. 156–200.

Brevoortia patronus and *B. gunteri* occurred in the area. The latter species spawned in February 1956.

Simmons, Ernest G., and Joseph P. Breuer.

1962. A study of redfish, *Sciaenops ocellata* Linnaeus, and black drum, *Pogonias cromis* Linnaeus. Publications of the Institute of Marine Science, Texas, vol. 8, pp. 184–211.

Incidence of occurrence of *Brevoortia* was 0.23 percent in the stomach contents of 1,197 redfish from Rockport, Tex.

Simmons, Ernest G., and H. Dickson Hoese.

1959. Studies on the hydrography and fish migrations of Cedar Bayou, a natural tidal inlet on the central Texas coast. Publications of the Institute of Marine Science, Texas, vol. 6, pp. 56–80.

Brevoortia sp. ranked eighth in list of fishes taken by fish trap, 1950–51.

Sindermann, Carl J.

1961. Serological techniques in fishery research. Transactions of the 26th North American Wildlife and Natural Resources Conference, pp. 298–309.

Relationship of *Brevoortia* to western Atlantic clupeids, *Alosa* and *Clupea*.

Skud, Bernard E., and William B. Wilson.

1960. Role of estuarine waters in gulf fisheries. Transactions of the 25th North American Wildlife and Natural Resources Conference, pp. 320–326.
Brevoortia mentioned.

Smith, Keith A.

1961. Air-bubble and electrical-field barriers as aids to fishing. Proceedings of the Gulf and Caribbean Fisheries Institute, 13th Annual Session, 1960, pp. 73–86.
Behavior of menhaden during fishing trials.

Sparks, Albert K.

1958. Some digenetic trematodes of fishes of Grand Isle, Louisiana. Proceedings of the Louisiana Academy of Science, vol. 20, pp. 71–82.
Parasites of *Brevoortia patronus*.

Springer, Victor G.

1960. Ichthyological surveys of the lower St. Lucie and Indian Rivers, Florida east coast. Florida State Board of Conservation, Marine Laboratory Report No. 60–16, 17 pp. (Processed).
Brevoortia tyrannus and *B. smithi* reported.

Springer, Victor G., and Kenneth D. Woodburn.

1960. An ecological study of the fishes of the Tampa Bay area. Florida State Board of Conservation, Marine Laboratory, Professional Papers Series No. 1, 104 pp.
Brevoortia patronus, *B. smithi*, and *B. tyrannus* larvae and juveniles reported from Florida.

Sproston, Nora G.

1946. A synopsis of the monogenetic trematodes. Transactions of the Zoological Society of London, vol. 25, pt. 4, pp. 185–600.
Parasites of *Brevoortia tyrannus* mentioned.

Steindachner, Franz.

1869. Ichthyologische Notizen (IX). Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschafliche Klasse, Band 60, Abt. 1, pp. 290–318.
Clupea (*Alosa*) *notocanthoides* original description from Mazatlan, Mexico.

1882. Beiträge zur Kenntniss der Fische Afrika's und Beschreibung einer neuen *Paraphoxinus*—Art aus der Herzegowina. Denkschriften der Kaiserlichen Akademie der Wissenschaften Mathematisch-Naturwissenschafliche Klasse, Band 45, pp. 1–18.
Clupea (*Alosa*) *setosa* from Liberia, Sherbero, and Gabun.

1895. Die Fische Liberia's. Notes from Leyden Museum, vol. 16, No. 1, pp. 1–96.
Clupea senegalensis described.

Steven, G. A.

1947. Report on the fisheries of Sierra Leone. Crown Agents, London, 66 pp.
General account of the fishery for *Ethmalosa fimbriata*.

Sutherland, Doyle F.

1958. Use of diagnostic X-ray for determining vertebral numbers of fish. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 244, 9 pp.
Methods and equipment for making X-ray photographs of menhaden.

1963. Variation in vertebral numbers of juvenile Atlantic menhaden. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 435, 21 pp.
Analysis of variance of mean vertebral numbers of *Brevoortia tyrannus* indicated two subpopulations along the Atlantic Coast of the United States.

Suttkus, Royal D.

1958. Distribution of menhaden in the Gulf of Mexico. Transactions of the 23rd North American Wildlife Conference, pp. 401–410.
Proportional measurements and meristic counts of 23 specimens of *Brevoortia smithi*.

Suttkus, Royal D., and Bangalore I. Sundararaj.

1961. Fecundity and reproduction in the largescale menhaden, *Brevoortia patronus* Goode. Tulane Studies in Zoology, vol. 8, No. 6, pp. 177–182.
Age, sexual maturity, and fecundity of *Brevoortia patronus* from examination of scales and ovaries.

Svetovidov, A. N.

1952. Sel'devye (Clupeidae). *In* Fauna SSSR, Ryby. Akadmii͡a Nauk SSSR, Zoologicheskiĭ Institut, tom 2, vyp. 1, 331 pp.
Inclusion of *Brevoortia*, *Ethmidium*, and *Ethmalosa* in a general account of the genera of clupeid fishes.

1953. O nekotorykh faktorakh, obuslovlivai͡ushchikh chislennost' sel'devykh. Akademii͡a Nauk SSSR, Ikhtiologicheskai͡a Komissii͡a, Trudy Soveshchanii, No. 1, pp. 99–109. (Trudy Vsesoi͡uznoĭ Konferent͡sii po Voprosam Rybnogo Khozi͡aĭstva, 1951.)
Brevoortia tyrannus mentioned among the clupeid fisheries of the world.

1961. Some factors determining the abundance of Clupeidae (O nekotorykh faktorakh, obuslovlivai͡ushchikh chislennost' sel'devykh), pp. 1–14. *In* Herring: Selected articles from Soviet periodicals. Israel Program for Scientific Translations, Jerusalem.
English translation of Svetovidov, 1953.

1963. Clupeidae. *In* Fauna of U.S.S.R., Fishes. Zoological Institute of the Academy of Sciences of the U.S.S.R., vol. 2, No. 1, 428 p. Israel Program for Scientific Translations, Jerusalem.
English translation of Svetovidov, 1952.

Tabb, Durbin C., and Raymond B. Manning.

1961. A checklist of the flora and fauńa of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July, 1957 through September, 1960. Bulletin of Marine Science of the Gulf and Caribbean, vol. 11, No. 4, pp. 552–649.
Adults and juveniles of *Brevoortia smithi* reported.

1962. Aspects of the biology of northern Florida Bay and adjacent estuaries. *In* Durbin C. Tabb, David L. Dubrow, and Raymond B. Manning. The ecology of northern Florida Bay and adjacent

estuaries, pt. II, pp. 39–79. State of Florida Board of Conservation, Technical Series No. 39.

Juvenile *Brevoortia smithi* reported from Coot Bay Pond and adult *Brevoortia* sp. from Florida Bay.

Tagatz, Marlin E., and Donnie L. Dudley.

1961. Seasonal occurrence of marine fishes in four shore habitats near Beaufort, N.C., 1957–60. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 390, 19 pp.

Occurrence of juvenile *Brevoortia tyrannus* in haul seine collections. Reported among the more abundant fishes at each habitat location.

Thompson, Seton H.

1960. The commercial fisheries of the Gulf and South Atlantic—a report of progress. Proceedings of the Gulf and Caribbean Fisheries Institute, 12th Annual Session, 1959, pp. 1–4.

Brief mention of the research work on *Brevoortia tyrannus*.

1961. What is happening to our estuaries. Transactions of the 26th North American Wildlife and Natural Resources Conference, pp. 318–322.

Menhaden mentioned.

Thompson, Will F.

1916. Fishes collected by the United States Bureau of Fisheries steamer "*Albatross*" during 1888, between Montevideo, Uruguay, and Tome, Chile, on the voyage through the Straits of Magellan. Proceedings of the U.S. National Museum, vol. 50, No. 2133, pp. 401–476.

Brevoortia tyrannus reported from Montevideo. *Ethmidium*, new genus with *Clupea notocanthoides* Steindachner, as type. *Ethmidium caerulea* (Cuvier and Valenciennes) reported.

Tortonese, Enrico.

1942. Studio di una collezione di pesci proveniente da Valparaiso (Chile). Bollettino dei Musei di Zoologia e di Anatomia Comparata R. della Universita di Torino, vol. 69, serie 4, No. 129, 26 pp.

Ethmidium caeruleum listed.

1951. Materiali per 10 studio sistematico e zoogeografico dei pesci della coste occidentali del Sud America. Revista Chilena de Historia Natural, Pura y Aplicada, Años 51–53, pp. 83–118.

Ethmidium maculatum listed and *E. chilcae* mentioned.

Valenciennes, Achille.

See Cuvier, Georges, and Achille Valenciennes, 1847.

Von Ihering, H.

See Ihering, H. von, 1897.

Walford, Lionel A.

1958. Living resources of the sea. Roland Press Co., New York, 321 pp.

Brief mention of oil yield, parasites, and electrofishing of menhaden.

Watts, J. C. D.

1962. Evidence of over-fishing in the Sierra Leone trawl fishery. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 24, No. 3, pp. 909–912.

Brief mention of Longhurst, 1960b.

1963. A note on *Ethmalosa fimbriata* (Bowd.) from Sierra Leone. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 25, No. 1, pp. 235–237.

A brief summary of fishery and biology of *Ethmalosa fimbriata* with the common names for immature, mature, and extra large fish in Sierra Leone.

Yañez Andrade, Parmenio.

1955. Peces utiles de la costa chilena. Revista de Biología Marina, Valparaiso, vol. 6, Nos. 1–3, pp. 29–81.

Brief description of *Ethmidium maculatum*.

INDEX BY SUBJECTS

Age and size:
  De Sylva, Kalber, and Shuster, 1962.
  June, 1961.
  June and Nicholson, 1963.
  June and Reintjes, 1959, 1960.
  June and Roithmayr, 1960.
  McHugh, 1960.
  McHugh, Oglesby, and Pacheco, 1959.
  Salzen, 1958.
  Suttkus and Sundararaj, 1961.
Alausa aurea: See *Brevoortia aurea.*
Alausa caerulea: See *Ethmidium.*
Alausa dorsalis: See *Ethmalosa fimbriata.*
Alausa maculata: See *Ethmidium maculatum.*
Alausa menhaden: See *Brevoortia tyrannus.*
Alausa pectinata: See *Brevoortia pectinata.*
Alausa tyrannus: See *Brevoortia tyrannus.*
Alosa caerulea: See *Ethmidium.*
Alosa maculata: See *Ethmidium maculatum.*
Alosa pectinata: See *Brevoortia pectinata.*
Atlantic menhaden: See *Brevoortia tyrannus.*

Bibliography:
  Butler, 1959, 1960.
  Christmas and Gunter, 1960.
  Devincenzi, 1920.
  Gunter and Christmas, 1960.
  Reintjes, Christmas, and Collins, 1960.
Bonga: *See Ethmalosa fimbriata.*
Brevoortia:
  Bailey, et al., 1960.
  Berg, 1940, 1947.
  Briggs, 1958.
  Christmas and Gunter, 1960.
  Cuvier and Valenciennes, 1847.
  De Buen, 1958.
  Devincenzi, 1920.
  Fowler, 1948.
  Gill, 1861.
  Gunter, 1958.
  Haskell, 1961.
  Hildebrand, 1948.
  June, 1961b.
  Lagler, Bardach, and Miller, 1962.
  Lunz, 1956.

- *Brevoortia*—Continued
  - Monod, 1961.
  - Nicol, 1960.
  - Regan, 1917.
  - Reintjes, 1960, 1961.
  - Reintjes, Christmas, and Collins, 1960.
  - Simmons and Hoese, 1959.
  - Svetovidov, 1952, 1963.
- *Brevoortia aurea:*
  - Angelescu and Boschi, 1959.
  - Beatty, 1959, 1961.
  - Campos Amaral, 1942.
  - Cuvier and Valenciennes, 1847.
  - De Buen, 1950, 1953.
  - De Carvalho, 1957.
  - De Olivera, 1942.
  - Dumeril, 1861.
  - Evermann and Kendall, 1906.
  - Fowler, 1911, 1942, 1948.
  - Goode, 1878, 1879.
  - Günther, 1868.
  - Hildebrand, 1948.
  - Hrytl, 1855.
  - Ihering, 1897.
  - Perugia, 1891.
  - Rochebrune, 1883.
  - Santos, 1952.
  - Silva, 1944.
  - Thompson, 1916.
- *Brevoortia chilcae: See Ethmidium chilcae.*
- *Brevoortia gunteri:*
  - Bailey, et al., 1960.
  - Breuer, 1962.
  - Briggs, 1958.
  - Bychowsky, 1957, 1961.
  - Christmas and Gunter, 1960.
  - Hargis, 1959.
  - Hedgpeth, 1957.
  - Hellier, 1962.
  - Hildebrand, 1948, 1958.
  - Hoese, 1958.
  - Hubbs, 1958.
  - Price, 1961.
  - Simmons, 1957.
- *Brevoortia maculata: See Ethmidium maculatum.*
- *Brevoortia patronus:*
  - Arnold, Wheeler, and Baxter, 1960.
  - Bailey, et al., 1960.
  - Breder, 1962.
  - Breuer, 1962.
  - Briggs, 1958.
  - Bullis, 1961.
  - Christmas, 1960.
  - Christmas and Gunter, 1960.
  - Christmas, Gunter, and Whatley, 1960.
  - Darnell, 1958, 1961, 1962.
  - Fowler, 1911.
  - Goode, 1878, 1879.
  - Gunter, 1958, 1961.
  - Gunter and Demoran, 1961.
  - Gunter and Shell, 1958.
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  - Hargis, 1959.
  - Hellier, 1962.
  - Hildebrand, 1948.
  - Hoese, 1958.
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  - Marvin and Lansford, 1962.
  - Price, 1961.
  - Richmond, 1962.
  - Simmons, 1957.
  - Sparks, 1958.
  - Springer and Woodburn, 1960.
  - Suttkus, 1958.
  - Suttkus and Sundararaj, 1961.
- *Brevoortia pectinata:*
  - Berg, 1895.
  - De Buen, 1950, 1953.
  - Devincenzi, 1920, 1924, 1925.
  - Devincenzi and Barattini, 1928.
  - Cuvier and Valenciennes, 1847.
  - Evermann and Kendall, 1906.
  - Fowler, 1940, 1942, 1951b.
  - Goode, 1878, 1879.
  - Günther, 1868.
  - Hildebrand, 1948.
  - Ihering, 1897.
  - Jenyns, 1842.
  - Kner and Steindachner, 1866.
  - Larrañaga, 1923.
  - Reed, 1897.
  - Silva, 1944.
  - Thompson, 1916.
- *Brevoortia smithi:*
  - Bailey, et al., 1960.
  - Briggs, 1958.
  - Christmas and Gunter, 1960.
  - Hildebrand, 1948.
  - Moody, 1961.
  - Reintjes, 1961, 1962.
  - Springer, 1960.
  - Springer and Woodburn, 1960.
  - Suttkus, 1958.
  - Tabb and Manning, 1961, 1962.
- *Brevoortia tyrannus:*
  - Arve, 1960.
  - Bailey, et al., 1960.
  - Bearden, 1961.
  - Behnke and Wetzel, 1960.
  - Berg, 1895.
  - Briggs, 1958.
  - Chipman, 1959, 1960.
  - Cuvier and Valenciennes, 1847.
  - De Sylva, Kalber, and Shuster, 1962.
  - Deubler, 1958.
  - Fowler, 1911, 1951b.
  - Gill, 1861.
  - Goode, 1878, 1879.
  - Gordon, 1961.
  - Grant, 1962.
  - Günther, 1868.
  - Halkett, 1913.

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Hall and McCutcheon, 1938.
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June and Chamberlin, 1959.
June and Nicholson, 1963.
June and Reintjes, 1959, 1960.
June and Roithmayr, 1960.
Kuntz and Radcliffe, 1917.
Lagler, Bardach, and Miller, 1962.
Leim and Day, 1959.
Mairs and Sindermann, 1962.
Mansueti, 1962.
Marak and Colton, 1961.
Marak, Colton, and Foster, 1962.
Marak, Colton, Foster, and Miller, 1962.
Massmann, 1954.
Massmann, Norcross, and Joseph, 1961, 1962.
McAllister, 1960.
McHugh, 1960.
McHugh, Oglesby, and Pacheco, 1959.
Milne-Edwards, 1840.
Pearcy and Richards, 1962.
Peck, 1894.
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Reintjes, 1961.
Richards, 1959, 1963a, 1963b, 1963c.
Roithmayr, 1962.
Schwartz, 1961.
Springer, 1960.
Springer and Woodburn, 1960.
Sproston, 1946.
Sutherland, 1958, 1963.
Svetovidov, 1952, 1953, 1961, 1963.
Tagatz and Dudley, 1961.

Classification:
Berg, 1940, 1947.
Cuvier and Valenciennes, 1847.
De Buen, 1958.
Fowler, 1942, 1948.
Hildebrand, 1948.
Monod, 1961.
Regan, 1917.
Svetovidov, 1952, 1963.
Clupanodon aureus: See *Brevoortia aurea.*
Clupea advena: See *Ethmidium.*
Clupea aurea: See *Brevoortia aurea.*
Clupea caerulea: See *Ethmidium.*
Clupea dorsalis: See *Ethmalosa fimbriata.*
Clupea fimbriata: See *Ethmalosa fimbriata.*
Clupea laccia vel 20-radiata: See *Brevoortia pectinata.*
Clupea pectinata: See *Brevoortia pectinata.*
Clupea maculata: See *Ethmidium maculatum.*
Clupea menhaden: See *Brevoortia tyrannus.*
Clupea notocanthus: See *Ethmidium chilcae.*
Clupea notocanthoides: See *Ethmidium chilcae.*
Clupea 20-radiata: See *Brevoortia pectinata.*
Clupea senegalensis: See *Ethmalosa fimbriata.*
Clupea setosa: See *Ethmalosa fimbriata.*
Common names:
Anonymous, 1948.
Bailey, et al., 1960.
Cadenat, 1947.
De Carvalho, 1957.
Delfin, 1902.
Hildebrand, 1948.
Silva, 1944.
Watts, 1963.

Distribution:
Briggs, 1958.
Christmas and Gunter,1960.
Hildebrand, 1948.
Reintjes, 1960.
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Kuntz and Radcliffe, 1917.
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Merriman and Sclar, 1952.
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Richards, 1959.
Ethmalosa dorsalis: See *Ethmalosa fimbriata.*
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Anonymous, 1948.
Bainbridge, 1957, 1960, 1961, 1962.
Blanc, 1948.
Boulenger, 1905.
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Cadenat, 1947, 1950, 1960.
Chabanaud and Monod, 1926.
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Longhurst, 1957, 1960a, 1960b, 1961.
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Mainguy and Doutre, 1958.
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Svetovidov, 1952.
Watts, 1963.

- *Ethmalosa* fishery:
  - Bainbridge, 1960.
  - Brown, 1948.
  - Cadenat, 1948.
  - Hornell, 1928.
  - Irvine, 1947.
  - Longhurst, 1960a, 1961.
  - Postel, 1950.
  - Steven, 1947.
  - Watts, 1963.
- *Ethmidium:*
  - Berg, 1940, 1947.
  - De Buen, 1958, 1959.
  - Delfin, 1900, 1902.
  - Cuvier and Valenciennes, 1847.
  - Gay, 1848.
  - Quijada B., 1913.
  - Reed, 1897, 1901.
  - Svetovidov, 1952.
  - Thompson, 1916.
- *Ethmidium chilcae:*
  - Abbott, 1899.
  - De Buen, 1958, 1959.
  - Delfin, 1900, 1902.
  - Dollo, 1904.
  - Cuvier and Valenciennes, 1847.
  - Gay, 1848.
  - Hildebrand, 1946.
  - Mann F., 1950, 1954.
  - Perez Canto, 1912.
  - Porter, 1909a, 1909b.
  - Quijada B., 1913.
  - Reed, 1897.
  - Steindachner, 1869.
  - Svetovidov, 1952.
  - Thompson, 1916.
  - Tortonese, 1942, 1951.
- *Ethmidium maculatum:*
  - Abbott, 1899.
  - Castillo and Vergara, 1907.
  - De Buen, 1958, 1959.
  - Delfin, 1900, 1902.
  - Fowler, 1940, 1944, 1945, 1951a.
  - Cuvier and Valenciennes, 1847.
  - Gay, 1848.
  - Mann F., 1950, 1954.
  - Oliver Schneider, 1943.
  - Perez Canto, 1912.
  - Quijada B., 1913.
  - Reed, 1897.
  - Regan, 1917.
  - Svetovidov, 1952.
  - Thompson, 1916.
  - Tortonese, 1942, 1951.
  - Yanez Andrade, 1955.

- Finescale menhaden: See *Brevoortia gunteri.*
- Food and feeding:
  - Anderson, Jonas, and Odum, 1958.
  - Bainbridge, 1957, 1960.
  - Chipman, 1959, 1960.
  - Darnell, 1958, 1961.
  - Deevey, 1956.
  - Harder, 1958, 1960.
  - Lagler, Bardach, and Miller, 1962.
  - Peck, 1894.
  - Richards, 1963b, 1963c.

- Gulf menhaden: See *Brevoortia patronus.*

- Lacha: See *Brevoortia pectinata* and *B. aurea.*
- Larvae and juveniles:
  - Arnold, Wheeler, and Baxter, 1960.
  - Bainbridge, 1961, 1962.
  - Breder, 1960, 1962.
  - Breuer, 1962.
  - Butler, 1959, 1960.
  - Chipman, 1959, 1960.
  - De Sylva, Kalber and Shuster, 1962.
  - Deubler, 1958.
  - Herman, 1963.
  - June, 1958.
  - June and Chamberlin, 1959.
  - Kuntz and Radcliffe, 1917.
  - Leim and Day, 1959.
  - Marak, Colton, Foster, and Miller, 1962.
  - Massmann, Norcross, and Joseph, 1961, 1962.
  - Merriman and Sclar, 1952.
  - Pearcy and Richards, 1962.
  - Reintjes, 1961, 1962.
  - Renfro, 1960.
  - Richards, 1959, 1963a, 1963b, 1963c.
  - Schwartz, 1961.
  - Simmons, 1957.
  - Springer and Woodburn, 1960.
  - Tabb and Manning, 1961, 1962.

- Machete: See *Ethmidium maculatum* or *E. chilcae.*
- Machuela: See *Ethmidium maculatum* or *E. chilcae.*
- Menhaden fishery:
  - Borgstrom, 1961.
  - Christmas, Gunter, and Whatley, 1960.
  - Cushing, et al., 1952.
  - Ellison, 1951.
  - Goode, 1879.
  - June, 1961a, 1961b.
  - June and Nicholson, 1963.
  - June and Reintjes, 1959, 1960.
  - McHugh, 1960.
  - Reintjes, 1960.
  - Reintjes and June, 1961.
  - Robas, 1959.
  - Roithmayr, 1963.
  - Rosen, 1959, 1960.
  - Rosen and Robinson, 1961, 1962a, 1962b.
  - Shuster, 1959.
  - Smith, 1961.
- Methods of capture:
  - See *Ethmalosa* fishery.
  - See Menhaden fishery.
  - Angelescu and Boschi, 1959.
  - Arve, 1960.

Methods of capture—Continued
Beatty, 1959, 1961.
Breder, 1960, 1962.
Bullis, 1961.
Haskell, 1961.
Hildebrand, 1958.
McHugh, 1960.
Reintjes, 1960.
Reintjes and June, 1961.
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Simmons and Hoese, 1959.
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Tagatz and Dudley, 1961.
Walford, 1958.
Morphology:
Doutre, 1959.
Gunter and Demoran, 1961.
Harder, 1958, 1960.
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Lagler, Bardach, and Miller, 1962.
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Occurrence in fresh water:
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Bychowsky, 1957, 1961.
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Hall and McCutcheon, 1938.
Lagler, Bardach, and Miller, 1962.
Mainguy and Doutre, 1958.
Mairs and Sindermann, 1962.
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Yellowfin menhaden: See *Brevoortia smithi.*

OCEAN MORTALITY AND MATURITY SCHEDULES OF KARLUK RIVER SOCKEYE SALMON AND SOME COMPARISONS OF MARINE GROWTH AND MORTALITY RATES

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ABSTRACT

Four population models representing different temporal distributions of natural mortality during the ocean life of Karluk sockeye salmon (*Onchorhynchus nerka*) are developed and discussed. The first model simulates a constant monthly instantaneous mortality rate throughout ocean life of sockeye. In the second model, the monthly instantaneous mortality rate is greatest during the first month of ocean residence and decreases arithmetically in each succeeding month. In the third model, the monthly instantaneous mortality rate decreases geometrically during the first 6 months of ocean life and remains constant thereafter. The fourth model simulates a "catastrophic", age-specific first-month instantaneous mortality rate and a constant, age-independent mortality rate in the second and succeeding months of ocean life.

Data collected on the releases and returns of marked Karluk sockeye in the late 1920's and early 1930's are used to estimate ocean mortality rates of the different fresh-water age groups of fish. The rates vary with the population model used, year of ocean life and fresh-water age. Mortality of the smaller, 3-fresh-water smolts is greater than for the larger, 4-fresh-water fish during at least a part of ocean residence.

Maturity schedules are estimated for 3- and 4-fresh-water smolts in each population model. Depending on the distribution of ocean mortality, from 53 to 62 percent of the 3-fresh-water fish and 74 to 80 percent of the 4-fresh-water sockeye achieve maturity by the end of their second year at sea.

The estimated instantaneous ocean mortality rates are compared with available estimates of Karluk sockeye ocean growth rates (weighted by the proportions of fish that mature as 1-, 2-, 3- and 4-ocean sockeye) on a monthly and annual basis to determine the net increase or decrease in weight during ocean residence. Except during the last year of ocean life of the relatively small fraction of Karluk sockeye that spend 4 years at sea, and then only for the first of 4 mortality distributions considered, ocean growth exceeds natural mortality.

The ranges of the estimated increases in bulk of Karluk sockeye during the first, second, and third years of ocean life, respectively, are 609 to 1,035 percent, 54 to 144 percent, and 26 to 84 percent. During the fourth year of ocean life, the bulk of Karluk sockeye is estimated to decrease by 8 to 10 percent under the first population model, and increase by 11 to 38 percent under the other 3 models.

The estimated percentage changes in bulk show that, except for the relatively scarce 4-ocean fish under the first population model, any capture of Karluk sockeye before the end of their ocean life causes a loss of potential yield, provided there exists an inshore fishery capable of catching the fish not needed for reproduction of the stock.

Information on the distribution and magnitude of ocean mortality of salmon and their maturity schedules is useful for comparing marine growth and mortality rates to determine the changes in bulk (net increase or decrease in weight) of a year class during ocean residence. Knowledge of changes in bulk, in turn, is useful for comparing salmon yields obtained by a pelagic fishery with the potential yields available to an inshore fishery.

Among the data available for studying the natural mortality of salmon during their ocean

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life are those reported by Barnaby (1944), who gives the details of a number of experiments involving the marking of sockeye smolts at Karluk River during the late 1920's and early 1930's and the enumeration of returns of marked fish to that river system after 1–4 years of ocean residence. These experiments provide an impressive array of population data that are particularly useful for estimating ocean mortality of salmon, because they were obtained before the development of a large-scale pelagic salmon fishery west of longitude 175° W. in the North Pacific Ocean and likely are free of the confounding effects of high seas fishing.

Ricker (1962) utilized certain data from the Karluk marking experiments in his excellent analysis of the ocean growth and mortality of sockeye salmon during their last 2 years at sea. Parker (1962) also used the Karluk data in his unique study of the ocean mortality of Pacific salmon. Much of Barnaby's experimental population data are used here in an ocean mortality analysis that differs from the analyses and results presented by Ricker and Parker, respectively, in that (a) a somewhat different mathematical model is used to estimate ocean mortality for the case where the mortality rate is assumed to be constant throughout ocean residence, and (b) estimates of ocean mortality are made for three situations where the rate is considered to vary during ocean residence.

The portion of Barnaby's experimental population data used in this paper consists of the releases and returns of smolts that were marked by the removal of the adipose and one or both of the ventral fins. This analysis will be primarily concerned with the two fresh-water age groups of Karluk sockeye that, according to Rounsefell (1958, table 17), account for over 95 percent of the annual run to that system. These are the 3- and 4-fresh-water smolts, or fish that migrate to sea in their third and fourth years of life respectively.[1]

For each of the four temporal distributions of ocean mortality considered in this study, I will estimate the percentages of 3- and 4-fresh-water smolts that mature after 1, 2, 3, and 4 years of ocean residence.

The estimates of ocean mortality presented here are compared with available growth rate data to determine changes in bulk of Karluk sockeye during ocean life. A number of such determinations are given in the last section of the paper. On the basis of these determinations, some inferences are drawn regarding the effects of high-seas fishing on the potential yield in weight of Karluk sockeye.

DURATION OF OCEAN RESIDENCE OF KARLUK SOCKEYE

Barnaby (1944) states that the major part of the seaward migration of Karluk sockeye takes place during the last week of May and the first 2 weeks of June each year. He also notes that the older smolts, that is, 4- and 5-fresh-water fish, migrate to sea earlier within the 3-week period of seaward migration than the younger smolts, that is, the 2- and 3-fresh-water fish. On the basis of these observations, I will assume for purposes of this study that 5-fresh-water smolts begin ocean life on June 1, 4-fresh-water smolts on June 5, 3-fresh-water smolts on June 10, and 2-fresh-water smolts on June 15.

From Rounsefell (1958, appendix table A–4) we can estimate the nearest dates ending in 5 or 0 on which 50 percent of the sockeye of different fresh-water and ocean ages return to the Karluk River. These estimates are given in table 1.

Using the dates of return given in table 1 as end points of ocean residence, the estimated duration of ocean life for each of 15 age groups of Karluk River sockeye is as shown in table 2.

For purposes of this study, it is assumed that the maximum ocean residence of 2- and 3-fresh-water smolts is 47.83 months, the maximum ocean residence of 4-fresh-water smolts is 48.17 months, and the maximum ocean residence of 5-fresh-water smolts is 36.50 months.

TABLE 1.—*Estimated dates on which 50 percent of the sockeye of different fresh-water and ocean ages return to Karluk River*

Fresh-water age group	Ocean age group [1]			
	1	2	3	4
2	July 15	June 30	June 15	June 10
3	Aug. 15	July 20	June 10	June 5
4	Sept. 5	Aug. 25	June 10	June 10
5	Sept. 10	Aug. 30	June 15	----------

[1] Ocean age is designated here as the nearest number of full years the fish spend in the ocean. A fish that spends, say, 26 months in the ocean is referred to as a 2-ocean fish.

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[1] Ricker (1962) refers to these two groups as 2- and 3-fresh-water sockeye respectively; Parker (1962) refers to them as 2- and 3-annuli smolts; Rounsefell (1958) refers to them as 3- and 4-year-old seaward migrants.

TABLE 2.—*Estimated duration of ocean residence, in months, of 15 age groups of Karluk River sockeye*

Fresh-water age group	Ocean age group			
	1	2	3	4
2	13.00	24.50	36.00	47.83
3	14.17	25.33	36.00	47.83
4	15.00	26.67	36.17	48.17
5	15.33	27.00	36.50	

RELEASES AND RETURNS OF MARKED KARLUK SOCKEYE SMOLTS

Barnaby (1944, tables 33–35, 37, 39, 41, and 43) reports the numbers of smolts of each fresh-water age group that were marked by the removal of the adipose and one or both of the ventral fins in seven different marking experiments between 1929 and 1933 at the Karluk River. He also shows the estimated returns of marked fish by ocean age for each experiment. Except for the correction of a few minor errors in the estimated returns and an added estimate of a return of 17 4-ocean fish from the 3-fresh-water smolts marked in the second experiment in 1930, Barnaby's data on releases and returns are shown in table 3.

EFFECT OF MARKING ON OCEAN SURVIVAL

The extent to which the removal of adipose-ventral fins affected the percentage returns of marked Karluk smolts cannot be determined from the Karluk sockeye data, since the entire smolt run was not counted in any year of marking and comparative survival rates of marked and unmarked smolts are not available. That the removal of adipose and ventral fins probably caused a differential mortality among marked Karluk smolts is indicated by results of experiments in other systems in which sockeye smolts were marked by the removal of adipose-ventral fin combinations. Ricker (1962), using data from Cultus Lake sockeye marking studies (Foerster, 1934, 1936, 1937), estimated that on a day-to-day basis, marked sockeye were about 27 percent more vulnerable to the causes of death in operation than unmarked fish. This means that the instantaneous ocean mortality rate of marked sockeye was about 1.27 times the instantaneous natural mortality rate encountered by unmarked sockeye during their ocean life.

For purposes of this study, I will use the factor 1.27 in estimating the instantaneous ocean mortal-

TABLE 3.—*Estimated releases and returns of Karluk River sockeye smolts marked by the removal of the adipose and one or both ventral fins.*

[Barnaby, 1944, tables 33–35, 37, 39, 41, and 43]

Year of release	Experiment number	Fresh-water age group	Group number	Estimated release (N_o)	Estimated returns					Estimated total percentage returns $(\Sigma R)/(N_o)$
					1-ocean (R_1)	2-ocean (R_2)	3-ocean (R_3)	4-ocean (R_4)	Total (ΣR)	
				Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Percent*
1929	1	3	1	21,858	656	2,882	450		3,988	18.24
		4	2	28,041	1,002	5,362	783		7,147	25.49
		5	3	162		22			22	13.58
1930	1	2	4	252			12		12	4.76
		3	5	14,676	28	1,730	725		2,483	16.92
		4	6	9,773	146	2,237	235		2,618	26.79
		5	7	299	5	62			67	22.41
	2	2	8	237						
		3	9	14,923	42	1,587	808	17	2,454	16.44
		4	10	9,554	208	2,396	160		2,764	28.93
		5	11	286		123			123	43.01
1931	1	2	12	84		23	23		46	54.76
		3	13	41,403	39	3,845	4,857	46	8,787	21.22
		4	14	8,145	119	2,349	339		2,807	34.46
		5	15	368		150			150	40.76
1932	1	3	16	6,275	13	833	339	11	1,196	19.06
		4	17	8,593	109	1,212	412	23	1,756	20.44
		5	18	132			4		4	3.03
	3	3	19	9,381		1,256	926	45	2,227	23.74
		4	20	5,580	50	594	306	12	962	17.24
		5	21	39						
1933	1	2	22	250		15	32		47	18.80
		3	23	25,394	7	3,208	1,441		4,656	18.34
		4	24	13,692	45	2,423	941		3,409	24.90
		5	25	664		77	29		106	15.96
Totals		2		823		38	67		105	12.76
		3		133,910	785	15,341	9,546	119	25,791	19.26
		4		83,378	1,679	16,573	3.176	35	21,463	25.74
		5		1,950	5	434	33		472	24.20

ity rates of unmarked Karluk sockeye from the release and return data given in table 3.

POPULATION MODEL 1

In this population model, the assumption is carried that the instantaneous ocean mortality rate of Karluk sockeye is constant throughout their ocean life. Notation is as follows:

N_o = The number of marked smolts of a given fresh-water age.

M = The monthly instantaneous mortality rate of unmarked sockeye during their ocean life.

1.27—A factor to adjust for the effects of marking on ocean survival.

t_1+k_1 = The number of full months (t_1) plus the additional fraction of a month (k_1) elapsing between the time of seaward migration and the return of mature 1-ocean fish to the Karluk River.

N_1 = The number of 1-ocean sockeye surviving at the end of t_1+k_1 months of ocean residence.

p_1 = The proportion of the surviving 1-ocean sockeye that mature and return to the Karluk River at the end of t_1+k_1 months.

R_1 = The number of 1-ocean sockeye that return to the Karluk River at the end of t_1+k_1 months of ocean residence.

$1-p_1$ = The proportion of the surviving 1-ocean sockeye that do not mature at the end of t_1+k_1 months of ocean residence.

N'_1 = The number of the surviving, immature 1-ocean sockeye at the end of t_1+k_1 months at sea.

t_2+k_2 = The number of full months (t_2) plus the additional fraction of a month (k_2) elapsing between the time of seaward migration and the return of mature 2-ocean fish to the Karluk River.

N_2 = The number of 2-ocean sockeye surviving at the end of t_2+k_2 months of ocean residence.

p_2 = The proportion of the surviving 2-ocean sockeye that mature and return to the Karluk River at the end of t_2+k_2 months.

R_2 = The number of 2-ocean sockeye that return to the Karluk River at the end of t_2+k_2 months of ocean residence.

$1-p_2$ = The proportion of the surviving 2-ocean sockeye that do not mature at the end of t_2+k_2 months of ocean residence.

N'_2 = The number of surviving, immature 2-ocean sockeye at the end of t_2+k_2 months at sea.

t_3+k_3 = The number of full months (t_3) plus an additional fraction of a month (k_3) elapsing between the time of seaward migration and the return of mature 3-ocean sockeye to the Karluk River.

N_3 = The number of 3-ocean sockeye surviving at the end of t_3+k_3 months of ocean residence.

p_3 = The proportion of the surviving 3-ocean sockeye that mature and return to the Karluk River at the end of t_3+k_3 months. (In the case of the 5-fresh-water smolts, t_3+k_3 is equal to 36.50 months, and p_3 is assumed to be equal to one.)

R_3 = The number of 3-ocean sockeye that mature and return to the Karluk River at the end of t_3+k_3 months of ocean residence.

$1-p_3$ = The proportion of the surviving 3-ocean sockeye that do not mature at the end of t_3+k_3 months of ocean residence.

N'_3 = The number of surviving, immature 3-ocean sockeye at the end of t_3+k_3 months of ocean residence.

t_4+k_4 = The number of full months (t_4) plus the additional fraction of a month (k_4) elapsing between the time of seaward migration and the return of mature 4-ocean sockeye to the Karluk River.

N_4 = The number of 4-ocean sockeye surviving at the end of t_4+k_4 months of ocean residence.

p_4 = The proportion of the surviving 4-ocean sockeye that mature and return to the Karluk River at the end of t_4+k_4 months of ocean residence. (In this study, it is assumed that the maximum ocean residence of 2-, 3- and 4-fresh-water smolts is t_4+k_4 months. Hence p_4 is assumed to be equal to one for these fresh-water age groups.)

R_4 = The number of 4-ocean sockeye that mature and return to the Karluk River at the end of t_4+k_4 months of ocean residence.

Identities among the foregoing quantities are as follows:

$$N_1=N_0e^{-1.27M(t_1+k_1)} \tag{1}$$

$$R_1=p_1N_1=p_1N_0e^{-1.27M(t_1+k_1)} \tag{2}$$

$$N'_1=(1-p_1)N_1=N_1-p_1N_1=N_1-R_1 \tag{3}$$

$$\begin{aligned} N_2&=N'_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]}\\ &=N_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]}\\ &\qquad -R_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]}\\ &=N_0e^{-1.27M(t_2+k_2)}-R_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \end{aligned} \tag{4}$$

$$\begin{aligned} R_2&=p_2N_2\\ &=p_2N_0e^{-1.27M(t_2+k_2)}\\ &\qquad -p_2R_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \end{aligned} \tag{5}$$

$$N'_2=(1-p_2)N_2=N_2-p_2N_2=N_2-R_2 \tag{6}$$

$$\begin{aligned} N_3&=N'_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]}\\ &=N_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]}-R_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]}\\ &=N_0e^{-1.27M(t_3+k_3)}-R_1e^{-1.27M[(t_3+k_3)-(t_1+k_1)]}\\ &\qquad -R_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \end{aligned} \tag{7}$$

$$\begin{aligned} R_3&=p_3N_3=p_3N_0e^{-1.27M(t_3+k_3)}\\ &\qquad -p_3R_1e^{-1.27M[(t_3+k_3)-(t_1+k_1)]}\\ &\qquad -p_3R_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \end{aligned} \tag{8}$$

$$N'_3=(1-p_3)N_3=N_3-p_3N_3=N_3-R_3 \qquad (9)$$

$$\begin{aligned}N_4=R_4&=N'_3e^{-1.27M[(t_4+k_4)-(t_3+k_3)]}\\&=N_3e^{-1.27M[(t_4+k_4)-(t_3+k_3)]}-R_3e^{-1.27M[(t_4+k_4)-(t_3+k_3)]}\\&=N_0e^{-1.27M(t_4+k_4)}-R_1e^{-1.27M[(t_4+k_4)-(t_1+k_1)]}\\&\qquad-R_2e^{-1.27M[(t_4+k_4)-(t_2+k_2)]}\\&\qquad\qquad-R_3e^{-1.27M[(t_4+k_4)-(t_3+k_3)]} \qquad (10)\end{aligned}$$

Equation (10), which is analogous to equation (11) of Parker (1962), can be used to estimate the monthly instantaneous ocean mortality rates for 2-, 3-, and 4-fresh-water smolts by entering observed or assumed quantities for N_0, R_1, R_2, R_3, R_4, t_1+k_1, t_2+k_2, t_3+k_3, and t_4+k_4 in the equation, and inserting trial values for M until one which results in a balanced expression is obtained. In a similar manner, equation (8) can be used to estimate M for 5-fresh-water smolts, since p_3 is assumed to be equal to one for this fresh-water age group.

Estimates of Monthly Instantaneous Mortality Rates

Of the 25 groups of marked sockeye smolts (table 3), there were 11 in which the numbers of fish released were small. These were the four groups of 2-fresh-water smolts and seven groups of 5-fresh-water smolts. The returns from each of these groups were also small in mumber, and they occurred in only 1 or 2 years following seaward migration. Because of the small numbers of fish involved, the instantaneous mortality rates are not estimated for the individual groups of 2- and 5-fresh-water smolts. Instead, the data for the four groups of marked 2-fresh-water smolts are combined, as are the data for the seven groups of marked 5-fresh-water smolts, for estimating the instantaneous ocean mortality rates for these two fresh-water age groups.

An estimate of the monthly instantaneous mortality rate can be obtained for each of the remaining 14 groups of marked sockeye, consisting of seven groups of 3-fresh-water smolts and seven groups of 4-fresh-water smolts.

Substitution of the appropriate t- and k-values in equations (10) and (8) yields the following expressions for estimating the monthly instantaneous ocean mortality rates for the four fresh-water age groups:

2-fresh-water smolts:
$$R_4=N_0e^{-60.74M}-R_1e^{-44.23M}-R_2e^{-29.63M}-R_3e^{-15.02M}$$
3-fresh-water smolts:
$$R_4=N_0e^{-60.74M}-R_1e^{-42.75M}-R_2e^{-28.58M}-R_3e^{-15.02M}$$
4-fresh-water smolts:
$$R_4=N_0e^{-61.18M}-R_1e^{-42.13M}-R_2e^{-27.30M}-R_3e^{-15.24M}$$
5-fresh-water smolts:
$$R_3=N_0e^{-46.36M}-R_1e^{-26.89M}-R_2e^{-12.06M}$$

The estimates of monthly instantaneous ocean mortality rates, as derived from the appropriate equations and release and return data, are given in table 4. The marked group numbers associated with the estimates are shown in parentheses.

Table 4.—*Estimated instantaneous ocean mortality rates of Karluk River sockeye, population model 1*

[Effects of marking adjusted by factor of 1.27]

Fresh-water age group	Monthly instantaneous ocean mortality rate (M)	Mean M for 3- and 4-fresh-water smolts	Standard deviation of mean M
2	0.0496 (Groups 4, 8, 12, and 22 combined).	----------	----------
3	0.0520 (1); 0.0480 (5); 0.0477 (9); 0.0381 (13); 0.0445 (16); 0.0365 (19); 0.0455 (23).	0.0446	0.0021
4	0.0402 (2); 0.0380 (6); 0.0366 (10); 0.0303 (14); 0.0426 (17); 0.0456 (20); 0.0369 (24).	.0386	.0018
5	0.0402 (Groups 3, 7, 11, 15, 18, 21, and 25 combined).	----------	----------

Relation Between Monthly Instantaneous Mortality Rate and Age and Size of Smolts

The estimates of monthly instantaneous ocean mortality rates shown in table 4 indicate a general decrease with an increase in the fresh-water age of smolts: 0.0496 for 2-fresh-water smolts; an average of 0.0446 for 3-fresh-water smolts; an average of 0.0386 for 4-fresh-water smolts; and 0.0402 for 5-fresh-water smolts. Since the estimates for the 2- and 5-fresh-water smolts are based on relatively small numbers of fish, they should, in a comparison of ocean mortality rate with age at time of outmigration, be considered as rough approximations. Each of the estimated average mortality rates for the 3- and 4-fresh-water smolts on the other hand are based on seven groups of marked sockeye. Each group contained large numbers of marked fish. Six of seven paired groups, that is, two groups of smolts marked in the same way in the same year, showed a higher ocean mortality rate for 3-fresh-water smolts than for 4-fresh-water smolts. The standard deviations of the means show that the difference between the mean mortality rates for 3- and 4-fresh-water smolts is significant at about the 85 percent confidence level.

From Barnaby (1944, table 27), we can estimate the average body length of fish in each of the four fresh-water age groups of smolts in the seaward migration through the week ending June 14 for the years 1929 to 1933 combined. The average lengths for the 2-, 3-, 4-, and 5-fresh-water smolts were 108, 131, 143, and 146 millimeters, respectively. Plotting the estimated monthly instantaneous mortality rates for the four fresh-water age groups against average lengths of smolts at time of seaward migration, as in figure 1, we see a general decrease in ocean mortality as size of smolts increases.

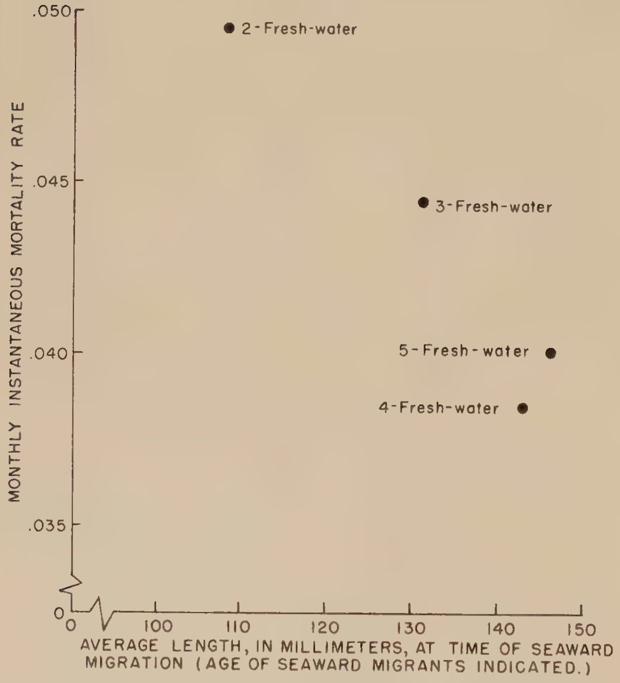

Figure 1.—Estimates of monthly instantaneous ocean mortality rates for Karluk sockeye of different lengths at time of seaward migration. (Data from table 4, and Barnaby, 1944, table 27).

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

The mortality rates for the different ocean age groups and ocean years of life of 3- and 4-fresh-water smolts, the two fresh-water age groups which account for practically the entire run of Karluk sockeye, can be estimated from the average monthly instantaneous ocean mortality rates (table 4) and estimates of the duration of ocean residence of different ocean age groups (table 2).

For sockeye of a given fresh-water age that mature at ocean age x, the total ocean mortality rate is estimated from the expression:

$$a_x = 1 - e^{-M(t_x + k_x)}$$

where t_x is the number of full months of ocean residence and k_x is the fraction of an additional month (if any) of ocean residence.

The annual ocean mortality rates during the first, second, third, and fourth years of ocean residence of sockeye of a given fresh-water age are obtained from the following expression:

$$a'_x = 1 - e^{-M[(t_x + k_x) - (t_{x-1} + k_{x-1})]}$$

where the quantity $[(t_x + k_x) - (t_{x-1} + k_{x-1})]$ represents the number of months elapsing between the time that one ocean age group returns to the Karluk River and the time that the next ocean age group returns to the Karluk River. This quantity generally is not equal to 12 months, hence the annual ocean mortality rates usually apply to periods of time other than 12 months. For example, table 2 shows for 3-fresh-water smolts that 1-ocean mature sockeye spend an average of 14.17 months at sea, 2-ocean mature sockeye spend an additional 11.16 months at sea, and so forth. Only in the case of 4-ocean mature sockeye of the 4-fresh-water smolts do the fish spend 12 months more in the ocean than sockeye that mature in the preceding year.

Table 5 shows the total ocean mortality rates for each ocean age group and the annual mortality rates for each ocean year of life for 3- and 4-fresh-water smolts.

Table 5.—*Estimated mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 1*

Fresh-water age group	Average monthly instantaneous ocean mortality rate, M	Ocean age	Duration of ocean residence	Total instantaneous mortality rate	Total ocean mortality rate (a_x)	Duration of ocean year	Instantaneous ocean mortality rate during year	Annual ocean mortality rate (a'_x)
		Years	*Months*		*Percent*	*Months*		*Percent*
3	0.0446	1	14.17	0.6320	46.8	14.17	0.6320	46.8
		2	25.33	1.1297	67.7	11.16	.4977	39.2
		3	36.00	1.6056	79.9	10.67	.4759	37.9
		4	47.83	2.1332	88.2	11.83	.5276	41.0
4	.0386	1	15.00	.5790	44.0	15.00	.5790	44.0
		2	26.67	1.0295	64.3	11.67	.4505	36.3
		3	36.17	1.3962	75.2	9.50	.3667	30.7
		4	48.17	1.8594	84.4	12.00	.4632	37.1

The estimated total ocean mortality rates for 3-fresh-water smolts range from 46.8 percent for those sockeye that mature as 1-ocean fish to 88.2 percent for those that mature as 4-ocean fish. Corresponding estimates for 4-fresh-water smolts are 44.0 and 84.4 percent, respectively.

The annual mortality rates generally decreased with the progression of ocean years. This is due, of course, to a general decrease in the number of months elapsing between the times that one ocean age group matured and the next older ocean age group matured. If the durations of ocean residence were 12, 24, 36, and 48 months for the four ocean age groups, the annual ocean mortality rates would be approximately 41.4 percent for 3-fresh-water smolts and 37.1 percent for 4-fresh-water smolts.

Maturity Schedules of 3- and 4-Fresh-Water Smolts

The maturity schedules of the 3-and 4-fresh-water smolts, that is, the proportions of a given population of seaward migrants that mature after 1, 2, 3, and 4 years of ocean residence, can be roughly estimated from the ratios, $R_1/\Sigma R$, $R_2/\Sigma R$, $R_3/\Sigma R$, and $R_4/\Sigma R$, which can be obtained from table 3. Such ratios, however, do not account for the mortality that occurs among immature sockeye from one year to the next during their ocean life. As a result, the ratios, $R_1/\Sigma R$, and $R_2/\Sigma R$, are generally overestimates of the proportions of a given smolt migration that mature as 1- and 2-ocean fish. Conversely, $R_3/\Sigma R$ and $R_4/\Sigma R$ are generally underestimates of the proportions of a given smolt migration that mature as 3- and 4-ocean fish.

The factors, p_1, p_2, p_3, and p_4, in equations (2), (5), (8), and (10) represent the proportions of surviving 1-, 2-, 3-, and 4-ocean sockeye that mature at the end of the first, second, third, and fourth years of ocean residence. The equivalents of p_1, p_2, and p_3 are as follows:

$$p_1=R_1/N_0e^{-1.27M(t_1+k_1)} \tag{11}$$

$$p_2=R_2/\{N_0e^{-1.27M(t_2+k_2)}-R_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]}\} \tag{12}$$

$$p_3=R_3/\{N_0e^{-1.27M(t_3+k_3)}-R_1e^{-1.27M[(t_3+k_3)-(t_1+k_1)]} -R_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]}\} \tag{13}$$

The factor, p_4, is assumed to be equal to one. Except for p_1, these factors do not reflect the maturity schedules of a given smolt migration, because they do not account for the proportions of fish that matured in the preceding year or years.

Denoting the proportions of a given smolt migration that mature as 1-, 2-, 3-, and 4-ocean sockeye by p'_1, p'_2, p'_3, and p'_4, where $p'_1+p'_2+p'_3+p'_4=1$, we see that $p_1=p'_1$; $p_2=p'_2/(1-p'_1)$; $p_3=p'_3/(1-p'_1-p'_2)$; and $p_4=p'_4/(1-p'_1-p'_2-p'_3)$. Transposing we obtain the following expressions for p'_1, p'_2, p'_3, and p'_4:

$$p'_1=p_1 \tag{14}$$

$$p'_2=p_2(1-p'_1) \tag{15}$$

$$p'_3=p_3(1-p'_1-p'_2) \tag{16}$$

$$p'_4=1-p'_1-p'_2-p'_3 \tag{17}$$

Substitution of the appropriate values for (t_1+k_1), (t_2+k_2), and (t_3+k_3) in equations (11), (12), and (13) provides the following expressions for p_1, p_2, and p_3:

3-fresh-water smolts:

$$p_1=R_1/\{N_0e^{-18.00M}\}$$
$$p_2=R_2/\{N_0e^{-32.17M}-R_1e^{-14.17M}\}$$
$$p_3=R_3/\{N_0e^{-45.72M}-R_1e^{-27.72M}-R_2e^{-13.55M}\}$$

4-fresh-water smolts:

$$p_1=R_1/\{N_0e^{-19.05M}\}$$
$$p_2=R_2/\{N_0e^{-33.87M}-R_1e^{-14.82M}\}$$
$$p_3=R_3/\{N_0e^{-45.94M}-R_1e^{-26.89M}-R_2e^{-12.06M}\}$$

Using data from tables 3 and 4 to estimate p_1, p_2, and p_3 for each group of marked 3- and 4-fresh-water smolts, and inserting these estimates in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean fish. These are shown in table 6.

TABLE 6.—*Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 1*

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3	1.35	51.41	45.77	1.47
4	3.34	71.04	24.61	1.01

Approximately one-half of the 3-fresh-water smolts mature by the end of 2 years in the ocean, with most of the remainder maturing after 3 years in the ocean. Nearly 75 percent of the 4-fresh-water smolts mature by the end of the second year of ocean residence.

Total Ocean Mortality Rate For a Given Outmigration

The total ocean mortality rate for a given outmigration of sockeye smolts depends upon the magnitude of the mortality rates for the different ocean age groups and the proportions of seaward migrants that mature after 1, 2, 3, and 4 years of ocean residence. The rate is represented by the expression:

$$a=1-p'_1(1-a_1)-p'_2(1-a_2) \\ -p'_3(1-a_3)-p'_4(1-a_4) \qquad (18)$$

where a_1, a_2, a_3, and a_4 are as shown in column 6 of table 5, and p'_1, p'_2, p'_3, and p'_4 are as shown in table 6. For 3-fresh-water smolts, the average total ocean mortality rate is 73.3 percent, and for 4-fresh-water smolts, the average total ocean mortality rate is 66.5 percent.

POPULATION MODEL 2

Data presented by Ricker (1962), as well as the data shown in figure 1 of this paper, strongly suggest that the ocean mortality of sockeye salmon is greater while the fish are small than it is when they become larger. Accordingly, it seems that a population model that accounts for a decreasing monthly instantaneous natural mortality rate with increasing size of fish, or cumulative time spent in the ocean, probably represents the actual survival conditions of sockeye salmon during their ocean life far better than a population model in which a constant natural mortality rate is assumed. In this section, we will consider a population model in which the monthly instantaneous natural mortality rate is a function of the number of months spent in the ocean by 3- and 4-fresh-water smolts.

The quantities N_0, R_1, R_2, R_3, R_4, p_1, p_2, p_3, p_4, t_1+k_1, t_2+k_2, t_3+k_3, and t_4+k_4 are as defined in Population Model 1. The factor 1.27 is used to adjust for the effects of marking. During the first month of a maximum of t_4+k_4 months of ocean residence, the instantaneous ocean mortality rate is represented by M_1. The instantaneous mortality rate during the second month of ocean residence is represented by M_2 and is assumed to be equal to $(1-d)M_1$, where d is equal to $1/(t_4+k_4)$. The instantaneous mortality rate during the third month of ocean residence is represented by M_3 and is assumed to be equal to $(1-2d)M_1$. In each succeeding month of ocean life, the instantaneous mortality rate is assumed to decrease by the quantity dM_1. The sequence of monthly instantaneous mortality rates is an arithmetic progression.

During month t_x of ocean life, the instantaneous mortality rate, M_{t_x}, is equal to $[M_1-(t_x-1)dM_1]$ or $M_1[1-(t_x-1)d]$. The instantaneous mortality rate for the fraction k_x of month (t_x+1) is $k_xM_1[1-(t_x)d]$. The rate for the remaining fraction $(1-k_x)$ of the month is $(1-k_x)M_1[1-(t_x)d]$. The sum of the monthly instantaneous mortality rates from the first month of ocean life through month t_x is $(t_x/2)(M_1+M_{t_x})$. Upon substitution for M_{t_x} and factoring, this sum is equivalent to $M_1(t_x/2)[2-(t_x-1)d]$. The sum of the monthly instantaneous ocean mortality rates from, say, month (t_1+2) through month t_2 is given by $[(t_2-t_1-1)/2][M_{t_1+2}+M_{t_2}]$. Upon substitution for M_{t_1+2} and M_{t_2} and factoring, this sum is equal to $M_1[(t_2-t_1-1)/2][2-(t_1+t_2)d]$. Thus, the returns of sockeye of different ocean ages are as shown by the following equations:

$$R_1=p_1N_0e^{-1.27M_1\left\{\frac{t_1}{2}[2-(t_1-1)d]+k_1[1-(t_1)d]\right\}} \qquad (19)$$

$$R_2=p_2N_0e^{-1.27M_1\left\{\frac{t_2}{2}[2-(t_2-1)d]+k_2[1-(t_2)d]\right\}} \\ -p_2R_1e^{-1.27M_1\left\{(1-k_1)[1-(t_1)d]+\frac{t_2-t_1-1}{2}[2-(t_1+t_2)d]+k_2[1-(t_2)d]\right\}} \qquad (20)$$

$$R_3=p_3N_0e^{-1.27M_1\left\{\frac{t_3}{2}[2-(t_3-1)d]+k_3[1-(t_3)d]\right\}}-p_3R_1e^{-1.27M_1\left\{(1-k_1)[1-(t_1)d]+\frac{t_3-t_1-1}{2}[2-(t_1+t_3)d]+k_3[1-(t_3)d]\right\}} \\ -p_3R_2e^{-1.27M_1\left\{(1-k_2)[1-(t_2)d]+\frac{t_3-t_2-1}{2}[2-(t_2+t_3)d]+k_3[1-(t_3)d]\right\}} \qquad (21)$$

$$R_4=N_0e^{-1.27M_1\left\{\frac{t_4}{2}[2-(t_4-1)d]+k_4[1-(t_4)d]\right\}}-R_1e^{-1.27M_1\left\{(1-k_1)[1-(t_1)d]+\frac{t_4-t_1-1}{2}[2-(t_1+t_4)d]+k_4[1-(t_4)d]\right\}} \\ -R_2e^{-1.27M_1\left\{(1-k_2)[1-(t_2)d]+\frac{t_4-t_2-1}{2}[2-(t_2+t_4)d]+k_4[1-(t_4)d]\right\}}-R_3e^{-1.27M_1\left\{(1-k_3)[1-(t_3)d]+\frac{t_4-t_3-1}{2}[2-(t_3+t_4)d]+k_4[1-(t_4)d]\right\}} \qquad (22)$$

Equation (22) can be used to solve for M_1 for the 3- and 4-fresh-water smolts by the trial method used in Population Model 1. Values for t_1, k_1, t_2, k_2, t_3, k_3, t_4, and k_4 can be obtained from table 2, and the values for N_0, R_1, R_2, R_3, and R_4 from table 3. For 3-fresh-water smolts, d is equal to 1/47.83 or 0.020907; for 4-fresh-water smolts, d is equal to 1/48.17 or 0.020760. Substitution of the appropriate t-, k-, and d-values in equation (22) yields the following expressions for estimating M_1:

3-fresh-water smolts:

$$R_4=N_0e^{-31.00M_1}-R_1e^{-15.49M_1}-R_2e^{-7.02M_1}-R_3e^{-2.01M_1}$$

4-fresh-water smolts:

$$R_4=N_0e^{-31.22M_1}-R_1e^{-14.99M_1}-R_2e^{-6.38M_1}-R_3e^{-2.06M_1}$$

Estimates of Monthly Instantaneous Mortality Rates

Each of the seven groups of marked 3-fresh-water smolts provides an estimate of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their third year of life. Seven groups of marked 4-fresh-water smolts provide estimates of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their fourth year of life. These estimates, their averages, and the standard deviations of the means are shown in table 7. The marked group numbers associated with the estimates are shown in parentheses.

Using the averages in table 7 as the instantaneous mortality rates of 3- and 4-fresh-water smolts during their first month of ocean residence, we can estimate the mortality rates in any ocean month, m, as follows:

$$M_m=M_1[1-(m-1)d] \qquad (23)$$

TABLE 7.—*Estimates of first-month instantaneous ocean mortality rates for 3- and 4-fresh-water smolts, Karluk River sockeye, population model 2*

[Effects of marking adjusted by factor of 1.27]

Fresh-water age group	First-month instantaneous ocean mortality rate, M_1	Average	Standard deviation of mean
3	0.0720 (1); 0.0695 (5); 0.0700 (9); 0.0575 (13); 0.0648 (16); 0.0545 (19); 0.0660 (23).	0.0649	0.0025
4	0.560 (2); 0.0529 (6); 0.0504 (10); 0.0424 (14); 0.0619 (17); 0.0673 (20); 0.0534 (24).	.0549	.0030

Table 8 gives the instantaneous mortality rates for each month of ocean residence for the two fresh-water age groups.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

From the estimated monthly instantaneous ocean mortality rates given in table 8, we obtain estimates of the mortality rates for each ocean age group and ocean year as shown in table 9.

The estimated total ocean mortality rates for 3-fresh-water smolts range from 54.7 percent for those fish that mature as 1-ocean sockeye to 79.5 percent for those fish that mature as 4-ocean sockeye. Corresponding estimates for the 4-fresh-water smolts are 50.5 and 74.1 percent respectively.

Under this population model, the annual ocean mortality rates for 3-fresh-water smolts decrease from 54.7 percent during the first year (14.17 months) of ocean residence to 9.8 percent during the fourth year (11.83 months) of ocean residence. For 4-fresh-water smolts, the annual mortality rate decreases from 50.5 percent during the first year of ocean residence to 8.5 percent during

TABLE 8.—*Estimated monthly instantaneous ocean mortality rates for 3- and 4-fresh-water smolts, Karluk River sockeye, population model 2*

Month at sea (m)	Instantaneous mortality rate, fresh-water age group		Month at sea (m)	Instantaneous mortality rate, fresh-water age group		Month at sea (m)	Instantaneous mortality rate, fresh-water age group		Month at sea (m)	Instantaneous mortality rate, fresh-water age group	
	3	4		3	4		3	4		3	4
1	0.0649	0.0549	13	0.0486	0.0412	25	0.0323	0.0275	37	0.0160	0.0139
2	.0635	.0538	14	.0473	.0401	26	.0310	.0264	38	.0147	.0127
3	.0622	.0526	15	.0459	.0389	27	.0296	.0253	39	.0133	.0116
4	.0608	.0515	16	.0445	.0378	28	.0283	.0241	40	.0120	.0104
5	.0595	.0503	17	.0432	.0367	29	.0269	.0230	41	.0106	.0093
6	.0581	.0492	18	.0418	.0355	30	.0256	.0218	42	.0093	.0082
7	.0568	.0481	19	.0405	.0344	31	.0242	.0207	43	.0079	.0070
8	.0554	.0469	20	.0391	.0332	32	.0228	.0196	44	.0066	.0059
9	.0540	.0458	21	.0378	.0321	33	.0215	.0184	45	.0052	.0048
1	.0527	.0446	22	.0364	.0310	34	.0201	.0173	46	.0038	.0036
1	.0513	.0435	23	.0350	.0298	35	.0188	.0161	47	.0025	.0025
1	.0500	.0424	24	.0337	.0287	36	.0174	.0150	48	.0011	.0013
									49		.0002

TABLE 9.—*Estimated ocean mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 2*

[Effects of marking adjusted by factor of 1.27]

Fresh water age group	Ocean age	Duration of ocean residence	Total instantaneous mortality rate	Total ocean mortality rate (a_x)	Duration of ocean year	Instantaneous mortality rate during year	Annual ocean mortality rate (a'_x)
	Years	*Months*		*Percent*	*Months*		*Percent*
3	1	14.17	0.7929	54.7	14.17	0.7929	54.7
	2	25.33	1.2255	70.6	11.16	.4326	35.1
	3	36.00	1.4815	77.3	10.67	.2560	22.6
	4	47.83	1.5843	79.5	11.83	.1028	9.8
4	1	15.00	.7038	50.5	15.00	.7038	50.5
	2	26.67	1.0739	65.8	11.67	.3701	30.9
	3	36.17	1.2606	71.6	9.50	.1867	17.0
	4	48.17	1.3494	74.1	12.00	.0888	8.5

the fourth year of ocean residence. Most of the ocean mortality takes place during the first 14 or 15 months of ocean residence according to the estimates given in table 9.

MATURITY SCHEDULES

The maturity schedules for 3- and 4-fresh-water smolts under Population Model 2 are estimated by the procedure described under Population Model 1. Factorization and transposition of terms in equations (19) to (21) and substitution of appropriate values for the terms and sums of the arithmetic progressions in the exponents of these equations provide the following expressions for the proportions of surviving 1-, 2-, and 3-ocean sockeye that mature at the end of the first, second, and third years of ocean life:

3-fresh-water smolts:

$$p_1 = R_1/[N_0 e^{-15.52M_1}]$$
$$p_2 = R_2/[N_0 e^{-23.98M_1} - R_1 e^{-8.47M_1}]$$
$$p_3 = R_3/[N_0 e^{-28.99M_1} - R_1 e^{-13.48M_1} - R_2 e^{-5.01M_1}]$$

4-fresh-water smolts:

$$p_1 = R_1/[N_0 e^{-16.28M_1}]$$
$$p_2 = R_2/[N_0 e^{-24.84M_1} - R_1 e^{-8.56M_1}]$$
$$p_3 = R_3/[N_0 e^{-29.16M_1} - R_1 e^{-12.83M_1} - R_2 e^{-4.32M_1}]$$

Using data from tables 3 and 7 in the above expressions to obtain estimates of p_1, p_2, and p_3 for each group of marked 3- and 4-fresh-water smolts and inserting the resulting p-values in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean sockeye under Population Model 2. The average percentages are shown in table 10.

TABLE 10.—*Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 2*

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3	1.63	57.74	39.83	0.80
4	3.89	74.48	21.14	.49

Under Population Model 2, slightly higher proportions (approximately 4 to 7 percent) of the 3- and 4-fresh-water smolts mature by the end of 2 years of ocean life than under Population Model 1. The differences between the maturity schedules under Population Models 1 and 2 result from differences in the distribution of ocean mortality.

Total Ocean Mortality Rate for a Given Outmigration

The ocean mortality rate for a given outmigration of sockeye is the same under Population Model 2 as it was under Population Model 1. This rate is fixed, in our estimates, by the ratios of marked fish returning to those released. Redistribution of the monthly instantaneous ocean mortality rates does not affect it.

POPULATION MODEL 3

Population Models 1 and 2 deal with what might be considered as two extreme situations with regard to the temporal distribution of ocean mortality of Karluk sockeye. In one case we considered ocean mortality to be constant throughout the period of ocean residence. In the other case we considered ocean mortality to decrease continually throughout the period of ocean residence, becoming zero at the end of 4 years. In view of the evidence which suggests that the ocean mortality rate of sockeye is greater while they are small than it is when they become larger and in view of the lack of evidence that the ocean mortality rate continually decreases and becomes zero after an extended period of time, it seems worthwhile to examine what is intended to be an intermediate situation, one that we will consider under Population Model 3.

In this model it is assumed that the monthly instantaneous mortality rate decreases geometrically during the first 6 months of ocean residence such that M_2, the second-month mortality rate, is equal to $0.5M_1$, where M_1 is the first-month mortality rate; M_3, the third–month mortality rate, is equal to $0.5M_2$ or $0.25M_1$; M_4, the fourth-month mortality rate, is equal to $0.5M_3$ or $0.125M_1$; M_5, the fifth-month mortality rate, is equal to $0.5M_4$ or $0.0625M_1$; and M_6, the sixth-month mortality rate, is equal to $0.5M_5$ or $0.03125M_1$. It is further assumed that the instantaneous mortality rate during the seventh and each succeeding month of ocean residence is equal to M_6 or $0.03125M_1$.

The sum of the monthly instantaneous mortality rates during the first 6 months of ocean residence is $M_1+0.5M_1+0.25M_1+\ldots+0.03125M_1$, or $1.96875M_1$. The sum of the monthly instantaneous mortality rates during any number of months after the sixth month of ocean residence is the product of the number of months involved and $0.03125M_1$.

The quantities N_0, R_1, R_2, R_3, R_4, p_1, p_2, p_3, p_4, t_1+k_1, t_2+k_2, t_3+k_3, and t_4+k_4 are as defined in the previous models. The factor 1.27 is used to adjust for the effects of marking. Thus, the returns of sockeye of different ocean ages are as shown by the following equations:

$$R_1=p_1N_0e^{-1.27M_1[1.96875+(t_1+k_1-6)(0.03125)]} \tag{24}$$

$$R_2=p_2N_0e^{-1.27M_1[1.96875+(t_2+k_2-6)(0.03125)]} -p_2R_1e^{-1.27M_1[(t_2+k_2)-(t_1+k_1)](0.03125)} \tag{25}$$

$$R_3=p_3N_0e^{-1.27M_1[1.96875+(t_3+k_3-6)(0.03125)]} -p_3R_1e^{-1.27M_1[(t_3+k_3)-(t_1+k_1)](0.03125)} -p_3R_2e^{-1.27M_1[(t_3+k_3)-(t_2+k_2)](0.03125)} \tag{26}$$

$$R_4=N_0e^{-1.27M_1[1.96875+(t_4+k_4-6)(0.03125)]} -R_1e^{-1.27M_1[(t_4+k_4)-(t_1+k_1)](0.03125)} -R_2e^{-1.27M_1[(t_4+k_4)-(t_2+k_2)](0.03125)} -R_3e^{-1.27M_1[(t_4+k_4)-(t_3+k_3)](0.03125)} \tag{27}$$

Equation (27) is used to solve for M_1 for the 3- and 4-fresh-water smolts by the trial method mentioned previously. Substitution of the appropriate *t*- and *k*-values in equation (27) yields the following expressions for estimating M_1:

3-fresh-water smolts:

$$R_4=N_0e^{-4.16M_1}-R_1e^{-1.34M_1}-R_2e^{-0.89M_1}-R_3e^{-0.47M_1}$$

4-fresh-water smolts:

$$R_4=N_0e^{-4.17M_1}-R_1e^{-1.32M_1}-R_2e^{-0.85M_1}-R_3e^{-0.48M_1}$$

TABLE 11.—*Estimates of first-month instantaneous ocean mortality rates for 3- and 4-fresh-water smolts, Karluk River sockeye, population model 3*

[Effects of marking adjusted by factor of 1.27]

Fresh-water age	First-month instantaneous ocean mortality rate, M^1	Average	Standard deviation of mean
3	0.5224 (1); 0.5230 (5); 0.5279 (9); 0.4410 (13); 0.4870 (16); 0.4140 (19); 0.4976 (23).	0.4876	0.0167
4	0.4138 (2); 0.3953 (6); 0.3746 (10); 0.3181 (14); 0.4669 (17); 0.5114 (20); 0.4063 (24)	.4123	.0236

Estimates of Monthly Instantaneous Ocean Mortality Rates

Each of the seven groups of marked 3-fresh-water smolts and the seven groups of marked 4-fresh-water smolts (table 3) provides an estimate of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their third and fourth years of life. These estimates, their averages, and the standard deviations of the means, are shown in table 11. The marked group numbers associated with the estimates are shown in parentheses.

Using the averages in table 11 as the instantaneous mortality rates of 3- and 4-fresh-water smolts during their first month of ocean residence, we can obtain estimates of the mortality rates during the second through sixth months of ocean residence under Population Model 3 by multiplying M_1 by 0.5, 0.25, 0.125, 0.0625, and 0.03125, respectively. Table 12 gives the instantaneous mortality rates for each month of ocean residence for the two fresh-water age groups.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

From the estimated monthly instantaneous ocean mortality rates given in table 12, we obtain estimates of the mortality rates for each ocean age group and ocean year as shown in table 13.

TABLE 12.—*Estimated monthly instantaneous ocean mortality rates 3- and 4-fresh-water smolts, Karluk River sockeye, population model 3*

Month at sea	Instantaneous mortality rate	
	3-fresh-water fish	4-fresh-water fish
1st	0.4876	0.4123
2d	.2438	.2062
3d	.1219	.1031
4th	.0610	.0515
5th	.0305	.0258
6th and each succeeding month	.0152	.0129

TABLE 13.—*Estimated ocean mortality rates for each ocean age group and ocean year, 3- and 4-fresh–water smolts, Karluk River sockeye, population model 3.*

[Effects of marking adjusted by factor of 1.27]

Fresh water age group	Ocean age	Duration of ocean residence in months	Total instantaneous mortality rate	Total ocean mortality rate (a_x)	Duration of ocean year	Instantaneous mortality rate during year	Annual ocean mortality rate (a'_x)
	Years	*Months*		*Percent*	*Months*		*Percent*
3	1	14.17	1.0842	66.2	14.17	1.0842	66.2
	2	25.33	1.2538	71.4	11.16	.1696	15.6
	3	36.00	1.4160	75.7	10.67	.1622	15.0
	4	47.83	1.5958	79.7	11.83	.1798	16.4
4	1	15.00	.9279	60.5	15.00	.9279	60.5
	2	26.67	1.0784	66.0	11.67	.1505	14.0
	3	36.17	1.2010	69.9	9.50	.1226	11.5
	4	48.17	1.3558	74.2	12.00	.1548	14.3

The estimated total ocean mortality rates for 3-fresh-water smolts range from 66.2 percent for those fish that mature as 1-ocean sockeye to 79.7 percent for those fish that mature as 4-ocean sockeye. Corresponding estimates for the 4-fresh-water smolts, under this model, are 60.5 and 74.2 percent, respectively.

The annual ocean mortality rates for 3-fresh-water smolts decrease from 66.2 percent during the first year of ocean residence to 16.4 percent during the fourth year of ocean life. For 4-fresh-water smolts, the annual ocean mortality rate decreases from 60.5 percent during the first year of ocean life to 11.5 percent during the third year of ocean life and then increases to 14.3 percent during the longer fourth year of ocean residence.

Under this model, most of the ocean mortality takes place during the first 6 months of ocean residence.

Maturity Schedules

Factorization and transposition of terms in equations (24) to (26) and substitution of appropriate t- and k- values in the exponents of these equations provide the following expressions for the proportions of surviving 1-, 2-, and 3-ocean sockeye that mature at the end of the first, second, and third years of ocean life:

3-fresh-water smolts:

$$p_1 = R_1/[N_o e^{-2.82M_1}]$$
$$p_2 = R_2/[N_o e^{-3.27M} - R_1 e^{-0.44M_1}]$$
$$p_3 = R_3/[N_o e^{-3.69M_1} - R_1 e^{-0.87M_1} - R_2 e^{-0.42M_1}]$$

4-fresh-water smolts:

$$p_1 = R_1/[N_o e^{-2.86M_1}]$$
$$p_2 = R_2/[N_o e^{-3.32M_1} - R_1 e^{-0.46M_1}]$$
$$p_3 = R_3/[N_o e^{-3.70M_1} - R_1 e^{-0.84M_1} - R_2 e^{-0.38M_1}]$$

Using data from tables 3 and 11 in the foregoing expressions to obtain estimates of p_1, p_2, and p_3 for each group of marked 3- and 4-fresh-water smolts and inserting the resulting p-values in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean sockeye under Population Model 3. The average percentages are shown in table 14.

TABLE 14.—*Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 3*

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3	2.35	59.78	37.05	0.82
4	5.15	74.75	19.62	.48

Under this population model, approximately 2 or 3 percent more of the 3- and 4-fresh-water smolts mature by the end of the second year of ocean life than under Population Model 2.

POPULATION MODEL 4

It might be hypothesized that the difference between the ocean mortality rates of 3- and 4-fresh-water sockeye smolts is caused by some survival condition which operates differentially on small (3-fresh-water) and large (4-fresh-water) smolts early in the ocean lives of these fish, say, during the first month of ocean residence and that the mortality rate during succeeding months of ocean life is the same for the two fresh-water age groups. If this is the case, it would seem to follow that the first-month ocean mortality rates for both fresh-water age groups would be great in comparison with the mortality rates during the second and succeeding months of ocean life. In this section, we will consider a population model that simulates these survival conditions.

It is assumed that the first-month instantaneous ocean mortality rate of 4-fresh-water smolts, M_{1_4}, is 20 times M_{2_4}, their instantaneous mortality rate during the second and each succeeding month of ocean residence. The first-month instantaneous ocean mortality rate of 3-fresh-water smolts is represented by M_{1_3} or cM_{1_4}, where c measures the differential mortality caused by some survival condition. The mortality rate of 3-fresh-water smolts during the second and each succeeding month of ocean residence is assumed to be the same as for 4-fresh-water smolts, that is M_{2_4}, or 0.05 M_{1_4}.

The quantities N_0, R_1, R_2, R_3, R_4, p_1, p_2, p_3, p_4, t_1+k_1, t_2+k_2, t_3+k_3, and t_4+k_4 are as previously defined. The factor 1.27 is used to adjust for the effects of marking. Hence, the returns from the 4-fresh-water smolt migrations are as shown by the following expressions:

$$R_1=p_1N_0e^{-1.27M_{1_4}[1+(t_1+k_1-1)(0.05)]} \tag{28}$$

$$\begin{aligned} R_2=p_2N_0e^{-1.27M_{1_4}[1+(t_2+k_2-1)(0.05)]} \\ -p_2R_1e^{-1.27M_{1_4}(0.05)[(t_2+k_2)-(t_1+k_1)]} \end{aligned} \tag{29}$$

$$\begin{aligned} R_3=p_3N_0e^{-1.27M_{1_4}[1+(t_3+k_3-1)(0.05)]} \\ -p_3R_1e^{-1.27M_{1_4}(0.05)[(t_3+k_3)-(t_1+k_1)]} \\ -p_3R_2e^{-1.27M_{1_4}(0.05)[(t_3+k_3)-(t_2+k_2)]} \end{aligned} \tag{30}$$

$$\begin{aligned} R_4=N_0e^{-1.27M_{1_4}[1+(t_4+k_4-1)(0.05)]} \\ -R_1e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_1+k_1)]} \\ -R_2e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_2+k_2)]} \\ -R_3e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_3+k_3)]} \end{aligned} \tag{31}$$

The returns of 1-, 2-, 3-, and 4-ocean fish from the 3-fresh-water smolt migrations are represented by equations identical to (28) through (31) respectively except that c, rather than 1, appears as the first term inside the bracketed portion of the first exponent of each equation. Thus, the returns of 4-ocean fish from the 3-fresh-water smolts migrations are represented as follows:

$$\begin{aligned} R_4=N_0e^{-1.27M_{1_4}[c+(t_4+k_4-1)(0.05)]} \\ -R_1e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_1+k_1)]} \\ -R_2e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_2+k_2)]} \\ -R_3e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_3+k_3)]} \end{aligned} \tag{32}$$

Equation (31) is used to solve for the first-month instantaneous ocean mortality rate for the 4-fresh-water smolts by the trial method used in previous population models. Substitution of appropriate t- and k-values from table 2 reduces equation (31) to the following expression:

$$R_4=N_0e^{-4.26M_{1_4}}-R_1e^{-2.11M_{1_4}}-R_2e^{-1.36M_{1_4}}-R_3e^{-0.76M_{1_4}}$$

Estimates of Monthly Instantaneous Ocean Mortality Rates

Each of seven groups of marked 4-fresh-water smolts (table 3) provides an estimate of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their fourth year of life. These estimates, their average, and the standard deviation of the mean are shown in table 15. The marked group numbers associated with the estimates are given in parentheses.

TABLE 15.—*Estimates of first-month instantaneous ocean mortality rates for 4-fresh-water Karluk River sockeye smolts, population model 4*

[Effects of marking adjusted by factor of 1.27]

First-month instantaneous ocean mortality rate, M_{1_4}	Average, $\overline{M}_{1_4}$	Standard deviation of mean
0.4734 (2); 0.4501 (6); 0.4290 (10); 0.3608 (14); 0.5212 (17); 0.5656 (20); 0.4522 (24).	0.4646	0.0248

Based on the average first-month instantaneous ocean mortality rate of 0.4646, the estimated mortality rate of 4-fresh-water (and 3-fresh-water) smolts during the second and each succeeding month of ocean residence is 0.05 times 0.4646 or 0.0232.

Inserting the estimate of $\overline{M}_{1_4}$ and appropriate t- and k-values in equation (32), we obtain the following expression for the returns of 4-ocean fish from the seaward migrations of 3-fresh-water smolts:

$$R_4=N_0e^{-0.59c}e^{-1.38}-R_1e^{-0.99}-R_2e^{-0.66}-R_3e^{-0.35}$$

Transposing terms and taking logarithms, we obtain the following expression for c:

$$c=\ln\{[R_4+R_1e^{-0.99}+R_2e^{-0.66}+R_3e^{-0.35}]/N_0e^{-1.38}\}/-0.59$$

Each of seven groups of marked 3-fresh-water smolts (table 3) provides an estimate of c. Each estimate of c, in turn, can be multiplied by M_{1_4} to furnish an estimate of M_{1_3}, the first-month instantaneous ocean mortality rate for 3-fresh-water sockeye smolts. Table 16 shows the estimates of c and M_{1_3} for each marked group, the average first-month instantaneous ocean mortality rate, and the standard deviation of the mean mortality rate.

TABLE 16.—*Estimates of first-month instantaneous ocean mortality rates of 3-fresh-water Karluk River sockeye smolts, population model 4*

[Effects of marking adjusted by factor of 1.27]

Marked group No.	Coefficient of differential mortality, c	First-month instantaneous ocean mortality rate, M_{1_3}
1	1.67	0.7759
5	1.62	.7526
9	1.65	.7666
13	1.09	.5064
16	1.41	.6551
19	.95	.4414
23	1.47	.6830
Averages	1.41	0.6544
Standard deviation of mean mortality rate		.0500

Based on the averages given in table 16, the first month instantaneous ocean mortality rate of 3-fresh-water smolts is approximately 40 percent greater than the corresponding rate for 4-fresh-water smolts and about 28 times (1.41×20 or 0.6544/0.0232) greater than the instantaneous mortality rate during the second and each succeeding month of ocean residence for 3- and 4-fresh-water smolts.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

From the average first-month instantaneous ocean mortality rates given in tables 15 and 16, we obtain estimates of the mortality rates for each ocean age group and ocean year as shown in table 17.

TABLE 17.—*Estimated ocean mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 4*

[Effects of marking adjusted by factor of 1.27]

Fresh water age group	Ocean age	Duration of ocean residence	Total instantaneous mortality rate	Total ocean mortality rate (a_x)	Duration of ocean year	Instantaneous mortality rate during year	Annual ocean mortality rate (a'_x)
	Years	*Months*		*Percent*	*Months*		*Percent*
3	1	14.17	0.9599	61.7	14.17	0.9599	61.7
	2	25.33	1.2189	70.4	11.16	.2589	22.8
	3	36.00	1.4664	76.9	10.67	.2475	21.9
	4	47.83	1.7408	82.5	11.83	.2745	24.0
4	1	15.00	.7894	54.6	15.00	.7894	54.6
	2	26.67	1.0601	65.4	11.67	.2707	23.7
	3	36.17	1.2805	72.2	9.50	.2204	19.8
	4	48.17	1,5589	79.0	12.00	.2784	24.3

The estimated total ocean mortality rates range from 61.7 percent for those 3-fresh-water smolts that mature as 1-ocean fish to 82.5 percent for those that mature as 4-ocean sockeye. Corresponding estimates for the 4-fresh-water smolts are 54.6 and 79.0 percent, respectively.

The annual ocean mortality rates for 3-fresh-water smolts decrease from 61.7 percent during the first year of ocean life to about 22 to 24 percent during each of the last 3 years of ocean residence. For 4-fresh-water smolts, the annual ocean mortality rate decreases from 54.6 percent during the first year of ocean life to about 20 to 24 percent during each of the succeeding years.

Under this model, of course, most of the ocean mortality takes place during the first month of ocean residence.

Maturity Schedules

Expressions for the proportions of surviving 1-, 2-, and 3-ocean sockeye that mature at the end of the first, second, and third years of ocean life can be obtained from equations (28) to (30) for 4-fresh-water smolts and from analogous equations (not shown in the text) for 3-fresh-water smolts. These expressions, after substitution of appropriate t- and k-values, are as follows:

3-fresh-water smolts:

$$p_1 = R_1/[N_0 e^{-1.27M_{1_4}(c+0.6585)}]$$

$$p_2 = R_2/[N_0 e^{-1.27M_{1_4}(c+1.2165)} - R_1 e^{-0.7087M_{1_4}}]$$

$$p_3 = R_3/[N_0 e^{-1.27M_{1_4}(c+1.7500)} - R_1 e^{-1.3862M_{1_4}} - R_2 e^{-0.6775M_{1_4}}]$$

4-fresh-water smolts:

$$p_1 = R_1/[N_0 e^{-2.1590M_{1_4}}]$$

$$p_2 = R_2/[N_0 e^{-2.9000M_{1_4}} - R_1 e^{-0.7410M_{1_4}}]$$

$$p_3 = R_3/[N_0 e^{-3.5033M_{1_4}} - R_1 e^{-1.3443M_{1_4}} - R_2 e^{-0.6032M_{1_4}}]$$

Using data from tables 3, 15, and 16 in the above expressions to obtain estimates of p_1, p_2, and p_3 for each group of marked 3- and 4-fresh-water smolts, and inserting the resulting p-values in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean sockeye under Population Model 4. The average percentages are shown in table 18.

TABLE 18.—*Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 4*

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3	2.11	57.30	39.59	1.00
4	4.34	73.36	21.61	.69

The maturity schedules of 3- and 4-fresh-water smolts under this population model are very similar to those under Population Model 2.

COMPARISON OF OCEAN MORTALITY RATES

The estimated average monthly instantaneous mortality rates during the different years of ocean life of 3- and 4-fresh-water Karluk sockeye smolts under the four population models are compared in figures 2 and 3. Similar comparisons of the annual ocean mortality rates are given in figures 4 and 5.

The mortality rates obtained under Population Model 1 are lower during the first year of ocean life than those obtained under the other three models. The situation is reversed in the second year. In the third and fourth years of ocean residence, the mortality rates under Population Models 2, 3, and 4 are considerably lower than those obtained under Population Model 1. The

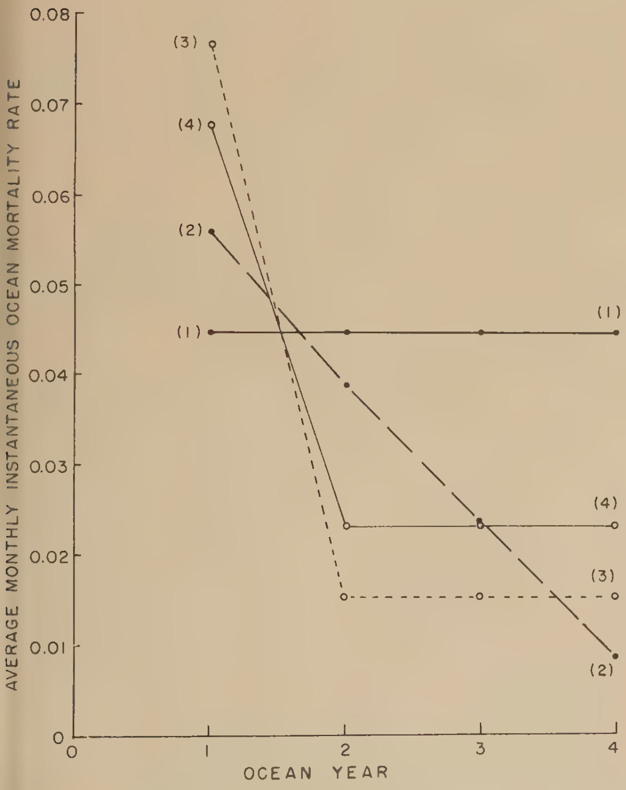

FIGURE 2.—Estimated average monthly instantaneous ocean mortality rates of 3-fresh-water Karluk River sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

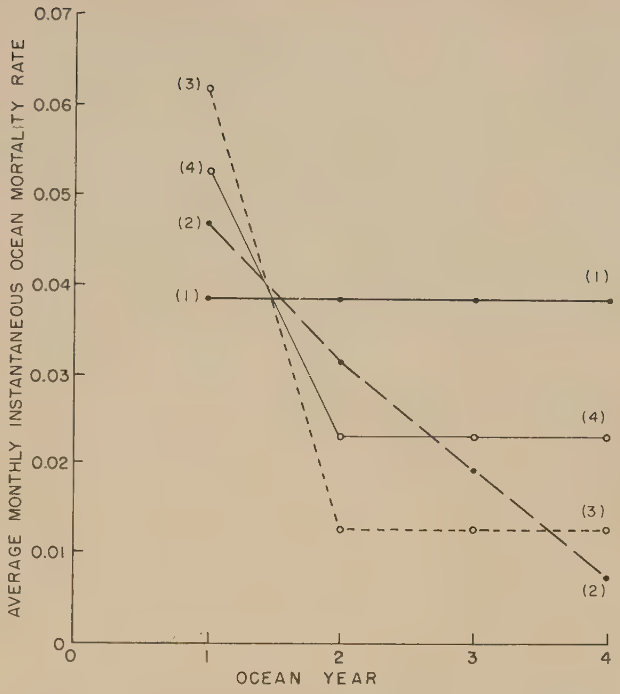

FIGURE 3.—Estimated average monthly instantaneous ocean mortality rates of 4-fresh-water Karluk sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

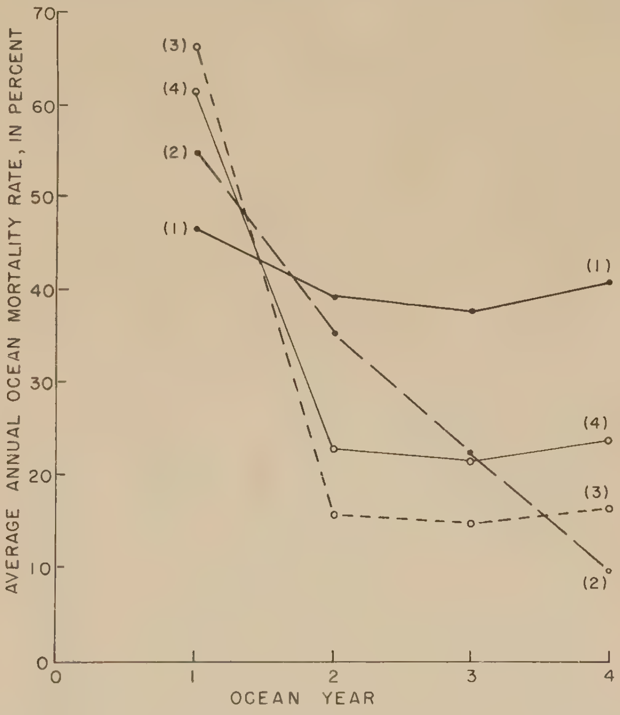

FIGURE 4.—Estimated average annual ocean mortality rates of 3-fresh-water Karluk sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

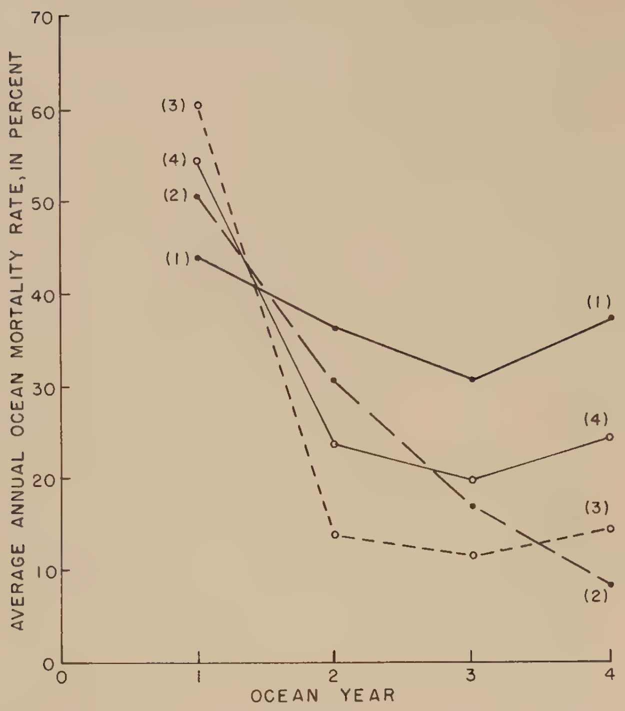

FIGURE 5.—Estimated average annual ocean mortality rates of 4-fresh-water Karluk sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

mortality rates during the first 3 years of ocean life are of principal interest, since only a minor fraction of the sockeye spend 4 years in the ocean.

DISCUSSION OF OCEAN MORTALITY RATES

The accuracy of the ocean mortality rate estimates presented here depends on the accuracy of the basic data used in the four population models and the validity of certain assumptions carried in the different models.

The numbers of sockeye in each marked group released were determined by counting the individual fish from which fins were removed. Since each marked fish was handled in the process of fin excision, the counting errors can be considered negligible.

The age composition of the marked smolts was estimated for each day of marking. Judging from Barnaby's report (1944, p. 272 and table 26), from 65 to 200 fish were sampled each day for this purpose. Seasonal total sample sizes ranged from about 1,000 to 2,000 fish. From this it would appear that the percentage error in the estimated numbers of marked smolts of a given fresh-water age in any experiment was quite small, probably less than 2 or 3 percent.

In an attempt to minimize any bias caused, for example, by early-running smolts of a given fresh-water age returning as late-running adults in subsequent seasons (or, as another example, late-running smolts of a given fresh-water age returning as early-running adults in subsequent seasons), smolts were marked throughout the period of seaward migration, and sampling for returning marked adults was carried out rigorously. It was found that the percentage occurrence of returning marked fish of each age group was fairly constant throughout the season (Barnaby, 1944, p. 282). This indicates that proportionate numbers of early-, middle-, and late-running adults of a given fresh-water age had been marked as smolts.

Enumeration of returns of marked fish involved sampling as large a portion as possible of each day's catch taken near the mouth of the Karluk River by beach seine, a type of gear generally considered to be relatively nonselective with respect to age or size of fish. The numbers of sockeye of pertinent ocean ages that were examined for marks from 1930 to 1937, together with the sampling ratios, can be calculated from Barnaby's tables 33, 34, 37, 39, and 43 and are as follows:

Year of sampling for marked fish	Ocean age groups of marked fish occurring in indicated year of sampling (Year of smolt migration shown in parentheses)	Estimated fish of indicated ocean ages in total run in year of sampling	Estimated fish of indicated ocean ages examined for marks	Mark sampling ratio
		Number	*Number*	*Percent*
1930	1 (1929)	182,053	891	0.5
1931	1 (1930); 2 (1929)	1,501,886	210,920	14.0
1932	1 (1931); 2 (1930); 3 (1929)	1,412,179	159,279	11.3
1933	1 (1932); 2 (1931); 3 (1930); 4 (1929).	1,812,577	178,080	9.8
1934	1 (1933), 2 (1932), 3 (1931); 4 (1930).	2,064,190	311,730	15.1
1935	2 (1933); 3 (1932); 4 (1931)	1,407,551	151,321	10.8
1936	3 (1933); 4 (1932)	330,985	41,257	12.5
1937	4 (1933)	0	0	--------

Except for 1930, approximately 10 to 15 percent of each year's total run of sockeye of the pertinent ocean age groups was examined for marks. The low sampling ratio in 1930 might account for the relatively large numbers of marked 1-ocean sockeye that were estimated to have returned from the 1929 releases of 3- and 4-fresh-water smolts.

The number of marked fish returning to the Karluk River were estimated on a weekly basis from catch statistics, weir counts, age composition of sockeye in the catch and escapement, and the proportions of marked fish occurring in the catch samples examined.

Judging from the large numbers of fish examined for marks (except in 1930), it is likely that the statistical errors involved in applying the sample ratios of marked-to-unmarked fish to the total run are very small. A procedural error, however, might have been introduced by misallocation of sockeye catches made in waters along the northwest coast of Kodiak Island. Misallocation of Karluk sockeye to other river systems would result in underestimates of the numbers of marked fish returning to the Karluk River and overestimates of ocean mortality. Misallocation of sockeye of other systems to the Karluk runs, on the other hand, would result in overestimates of the numbers of marked fish returning to the Karluk River and underestimates of ocean mortality.

On the basis of a tagging experiment on the western shore of Uganik Bay on Kodiak Island in 1927 (Rich and Morton, 1929), Barnaby (1944) considered all sockeye caught along the Kodiak Island coast between Cape Karluk (about 3 miles west of the mouth of the Karluk River) and West Point (about 6 miles inside the western shore of Uganik Bay and about 75 miles northeasterly from the mouth of the Karluk River) to have been fish originating in the Karluk River. Rich and Morton's study shows that some of the sockeye tagged in Uganik Bay were destined to areas other than the Karluk River. This indicates that some sockeye were misallocated to the Karluk runs by Barnaby's procedure. The extent to which this probable misallocation is compensated for by the allocation of Karluk sockeye caught outside the Cape Karluk-West Point area to other river systems cannot be accurately assessed. There is, however, some information available on this matter from unpublished catch statistics, tagging studies conducted in the late 1940's (Bevan, 1962), and escapement counts.

Donald E. Power and I have made a compilation of sockeye catch statistics for the Cape Karluk-West Point area for the years from 1930 to 1936. This compilation showed that approximately 70 percent of the total sockeye catch assigned to the Karluk River from 1930 to 1936 was taken between Cape Karluk and Cape Uyak, about 8 miles northeast of the mouth of the Karluk River. Thus, the bulk of the sockeye catch assigned to the Karluk River was taken within a relatively short distance from the mouth of the river.

Bevan (1962) shows that only a relatively small proportion of sockeye tagged in the area between Cape Karluk and Cape Uyak in 1948 was recovered in areas other than the Karluk River or near its mouth. This indicates that the great majority of sockeye caught in the Cape Karluk-Cape Uyak area were Karluk fish.

During the years 1930–36, when marked sockeye were returning to the Karluk River, approximately 60 percent of the estimated total Karluk sockeye runs consisted of fish that passed through the counting weir in the Karluk River. Thus, if all of the sockeye caught between Cape Karluk and Cape Uyak are considered to have originated in the Karluk River, those catches plus the escapements would account for about 88 percent (60 percent plus 0.7 times 40 percent) of the estimated total Karluk sockeye runs between 1930 and 1936. Of the remaining portion of the estimated total runs, that is, the sockeye caught between Cape Uyak and West Point, Rich and Morton (1929) show that a large proportion of the fish taken inside the mouth of Uganik Bay are Karluk sockeye. Bevan (1962) also shows that large proportions of the sockeye taken in the Cape Uyak-West Point area originate in the Karluk River.

That Barnaby's procedure for allocating catches to the Karluk sockeye runs likely resulted in a misallocation of Karluk fish to other river systems is indicated by the results of tagging experiments reported by Bevan (1962). Those experiments showed that large proportions of sockeye tagged outside the Cape Karluk-West Point area, namely, off Afognak Island in 1948 and off Uganik, Raspberry, and Afognak Islands in 1949, were fish that originated in the Karluk River. Bevan reports that from sockeye tagging at a wide variety of locations along the northwest coast of Kodiak Island, the Karluk system accounted for about 90 percent of the stream recoveries made on that coast.

On the basis of the foregoing information, it is reasonable to conclude that relatively small proportions of the estimated total Karluk sockeye runs from 1930 to 1936 consisted of fish originating in other river systems and that these small proportions were offset or more than offset by misallocation of Karluk sockeye to other systems.

A source of mechanical error in the estimates of marked sockeye returning to the Karluk River is the failure to detect all of the marked fish in the catch samples that were examined. No measure of such error is available for the Karluk experiments. It is an error, however, that is generally recognized to occur in marking studies. Such an error results in underestimates of numbers of marked fish returning and overestimates of ocean mortality rates.

The estimated durations of ocean residence probably contain some error. The errors, however, cannot be great since the smolts migrate to sea within a matter of a few weeks, and the estimated dates on which 50 percent of the fish in the different age groups return to the Karluk River are based on data for 27 years. In any event, an error of 1 or 2 months in estimating the durations of ocean residence would not affect the estimates of mortality very much.

The factor used to adjust for the effects of marking on survival perhaps should be some quantity other than 1.27. Just what, if any, alternative factor should be used is difficult to say, although it is highly unlikely that it should be less than 1.0. If no adjustment is made for the effects of marking, the instantaneous ocean mortality rates would be 1.27 times those rates obtained in the four population models. If the adjustment for marking mortality is increased, the instantaneous ocean mortality rates obtained in the four population models would be reduced. As Ricker (1962) points out, there is no theoretical upper limit that the adjustment can have.

If it is assumed that mortality due to marking takes place within a very short period of time after the marked fish are released, an adjustment for such mortality can be obtained from the ratio of percentage returns of marked and unmarked smolts. Although a considerable amount of evidence indicates that marked sockeye smolts suffer practically no mortality while being held for observation (Barnaby, 1944, and Foerster, 1937), I have estimated, for comparative purposes, the average monthly instantaneous ocean mortality rates of 3- and 4-fresh-water Karluk sockeye smolts, assuming an initial marking mortality of 60 percent and a constant ocean mortality rate. The estimate of initial loss is taken from data presented by Foerster (1934, 1936, and 1937) and as shown by Ricker (1962, table E, Appendix II). The average monthly instantaneous ocean mortality rates for the two fresh-water age groups of Karluk sockeye are approximately 0.026 and 0.017 which are considerably lower than corresponding estimates obtained in Population Model 1.

With regard to Population Model 1, available evidence strongly suggests that ocean mortality of sockeye is greater when the fish are small than it is when they become larger. Accordingly, it seems likely that the assumption of a constant ocean mortality rate results in an underestimate of ocean mortality during the early period of ocean residence and an overestimate during the later period of ocean life.

Concerning Population Model 2, it is rather unlikely that the ocean mortality rate decreases uniformly from month to month. It is also doubtful that the mortality of sockeye becomes negligible during the last several months of the fourth year of ocean residence. As for the first point, an arithmetic progression not only is a convenient method of representing a decreasing mortality rate but it also provides reasonably satisfactory estimates of the average monthly instantaneous mortality rates during the different ocean years of life even though the mortality rate does not decrease uniformly. As for the second point, relatively few Karluk sockeye would benefit from the low ocean mortality rates in the fourth year following seaward migration, because practically all of them mature after 2 or 3 years in the ocean.

Ocean mortality could be represented as a function of fish length or weight rather than time spent in the ocean in Population Model 2.

As indicated previously, Population Model 3 is intended to represent an intermediate situation with respect to the distributions of ocean mortality assumed in Population Models 1 and 2. From the standpoint of annual mortality rates (figs. 2 to 5), it does not depict the best intermediate situation. A lower rate of decrease in mortality during the first 6 months of ocean residence, combined with a constant ocean mortality rate thereafter, would provide annual mortality rates that lie between the estimates obtained in Population Models 1 and 2.

I am not aware of any information at this time upon which to judge the validity of the assumptions concerning ocean mortality in Population Model 4. For a situation such as that depicted in this model to occur would require a short-term, selective, intensive removal of smolts by predators near the mouth of the river, or a similar effect due to such factors as water temperature or salinity changes.

Some mention should be made of the fact that none of the population models presented here deals with situations such as where the mortality rate is considered to increase throughout the ocean life of sockeye or to be greater during the last month or two of ocean life of maturing sockeye than in preceding months or years.

The possibility that the mortality rate increases throughout the ocean life of sockeye salmon can be ruled out, I believe, on the basis of evidence from the Karluk marking experiments and for other sockeye populations (Ricker, 1962) that ocean mortality is greater during the early part of ocean residence than it is in later months and years.

It is of course possible that ocean mortality is greater during the last month or two of ocean life of maturing sockeye than in preceding months or years. Just what factor or factors might cause this to happen is difficult to say. As far as temporal effects of predation are concerned, smolts are subjected to considerable predation as they leave the river and enter the ocean. The size of the smolts probably renders them vulnerable to a variety of predators which cause little harm to adult sockeye. And, as Ricker (1962) mentions, although maturing sockeye are subject to predation by harbor seals and sea lions as they return to fresh water, they are leaving waters where the much more numerous fur seals occur.

Density-associated causes of mortality would seem to be less severe among maturing sockeye than smolt populations which are concentrated in small areas as they migrate to sea, and no more severe than for immature sockeye at sea.

Sockeye smolts appear to undergo at least as severe physical and chemical changes in their environment during their seaward migration as maturing sockeye undergo in their return to fresh water from the ocean.

Perhaps some physiological change associated with maturation causes an increased mortality among sockeye returning to fresh water. If so, t is not reflected in the general appearance of the ish. Sockeye taken in coastal waters are similar o maturing sockeye caught on the high seas nsofar as body brightness and firmness of flesh are concerned (personal communication with R. R. French). Nor does it result in a loss of body weight, according to data on growth rates given by Ricker (1962).

The foregoing considerations, of course, do not rule out the possibility that ocean mortality of maturing sockeye is greater during the last month or two of ocean life than in preceding months or years. In this connection, further investigation of the distribution and extent of ocean mortality of salmon is under way. For the time being, however, it should be noted, as Ricker (1962) notes with respect to his estimates of ocean mortality, that if the mortality during the last few months of ocean life of maturing salmon is greater than the estimates presented here, then the mortality rates during preceding months must be less than those estimated here, since the total mortality is fixed.

COMPARISON OF OCEAN GROWTH AND MORTALITY

Ricker (1962, Appendix tables A, B, and C), using data from Barnaby (1932), gives estimates of the instantaneous growth rates for nine Karluk sockeye fresh-water-ocean age groups during different years of ocean growth. These estimates, together with extrapolated estimates for some age groups not included in his tables, are shown in table 19.

The average instantaneous growth rates of 3- and 4-fresh-water sockeye during each of the 4 years of ocean growth can be estimated by weighting the individual estimates of g shown in table 19 by the proportions of sockeye that mature as 1-, 2-, 3-, and 4-ocean fish. Each of the four population models provides estimates of the weighted average annual growth rates of the two fresh-water age groups.

Using the maturity schedule obtained in Population Model 1 (table 6), the weighted average instantaneous growth rates of 3-fresh-water smolts during the first, second, third, and fourth years of ocean growth are estimated as follows:

$$\bar{g}_1=[3.159(.0135)+2.811(.5141)+2.894(1.4577)+2.650(.0147)]/1=2.8513$$

$$\bar{g}_2=[1.262(.5141)+1.053(.4577)+0.964(.0147)]/0.9865=1.1606$$

$$\bar{g}_3=[0.867(.4577)+0.794(.0147)]/0.4724=0.8647$$

$$\bar{g}_4=[0.434(.0147)]/0.0147=0.4340$$

TABLE 19.—*Estimated instantaneous growth rates of Karluk River sockeye during four ocean growth years*

[Data from Ricker (1962); see footnotes for details on estimates shown in parentheses]

Fresh-water age group	Ocean age	Growth rate (g) during ocean growth year:			
		1	2	3	4
	Years				
3	1	3. 159	----------	----------	----------
	2	2. 811	1. 262	----------	----------
	3	2. 894	1. 053	0. 867	----------
	4	[1] (2. 650)	[2] (0. 964)	[3] (0. 794)	[4] (0. 434)
4	1	2. 922	----------	----------	----------
	2	2. 655	. 974	----------	----------
	3	[5] (2. 548)	[6] (0. 927)	[7] (0. 763)	----------
	4	[8] (2. 333)	[9] (0. 849)	[10] (0. 699)	[11] (0. 382)

[1] $(2.650)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right](2.894)$

[2] $(0.964)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right](1.053)$

[3] $(0.794)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right](0.867)$

[4] $(0.434)=\frac{1}{3}\left[\frac{1.262}{2.811}+\frac{0.867}{1.053}+\frac{0.974}{2.655}\right][(0.794)]$

[5] $(2.548)=\frac{1}{3}\left[\frac{2.922}{3.159}+\frac{2.655}{2.811}+\frac{0.974}{1.262}\right](2.894)$

[6] $(0.927)=\frac{1}{3}\left[\frac{2.922}{3.159}+\frac{2.655}{2.811}+\frac{0.974}{1.262}\right](1.053)$

[7] $(0.763)=\frac{1}{3}\left[\frac{2.922}{3.159}+\frac{2.655}{2.811}+\frac{0.974}{1.262}\right](0.867)$

[8] $(2.333)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right][(2.548)]$

[9] $(0.849)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right][(0.927)]$

[10] $(0.699)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right][(0.763)]$

[11] $(0.382)=\frac{1}{3}\left[\frac{1.262}{2.811}+\frac{0.867}{1.053}+\frac{0.974}{2.655}\right][(0.699)]$

Using this procedure to estimate the weighted average growth rates of 4-fresh-water smolts during each year of ocean growth under Population Model 1 and to obtain corresponding estimates for the two fresh-water age groups under Population Models 2, 3, and 4, we obtain the set of weighted average instantaneous growth rates shown in table 20.

TABLE 20.—*Estimated weighted average instantaneous growth rates (g) of 3- and 4-fresh-water Karluk River sockeye smolts during 4 years of ocean growth, under population models 1, 2, 3, and 4*

Fresh-water age group	Year of ocean growth	Population model			
		1	2	3	4
3	1	2. 8513	2. 8484	2. 8486	2. 8496
	2	1. 1606	1. 1749	1. 1802	1. 1744
	3	. 8647	. 8656	. 8654	. 8652
	4	. 4340	. 4340	. 4340	. 4340
4	1	2. 6343	2. 6412	2. 6462	2. 6412
	2	. 9607	. 9630	. 9636	. 9625
	3	. 7605	. 7615	. 7615	. 7610
	4	. 3820	. 3820	. 3820	. 3820

In estimating the growth rates shown in table 20, the greatest weight is given to the growth rates for sockeye that mature after 2 or 3 years in the ocean. This means that in most cases the extrapolated estimates given in table 19 do not greatly affect the weighted averages. Also, with regard to the estimating procedure, the weighted growth rates are generally minimal values, since they represent the growth between the time that sockeye leave fresh water and the time that the first ocean annulus is formed, or the time between the formation of successive ocean annuli. The relatively rapid rates of growth that take place between the time the last ocean annulus is formed and the time that mature sockeye return to the Karluk River are not included in the estimates.

It is presumed here that the growth rates in each of the years of ocean growth pertain to periods of 12 months. Thus the duration of an ocean-growth-year differs somewhat from the durations of the ocean-mortality-years used in estimating mortality rates. To obtain a set of growth rate estimates that pertain to the time periods for which mortality estimates have been made, it is necessary to estimate the average monthly instantaneous growth rates in each ocean-growth-year and combine the resulting averages for parts of two ocean-growth-years. For example, the duration of the first year of ocean residence of 3-fresh-water fish has been estimated to be 14.17 months. The total instantaneous growth rate of 3-fresh-water smolts, under Population Model 1, during the first 14.17 months of ocean residence is estimated to be [(12) (2.8513)/12]+[(2. 17)(1.1606)/12], or 3.0612. The average monthly instantaneous growth rate during this period is, in turn, estimated to be 3.0612/14.17 or 0.2160. Also, for example, the duration of the second year of ocean residence of 3-fresh-water fish is considered to be 11.16 months. The total instantaneous growth rate of these fish during this period under Population Model 1 is estimated to be [(9.83) (1.1606)/12] plus [(1.33) (0.8647)/12], or 1.0465. The average monthly instantaneous growth rate is estimated to be 1.0465/11.16, or 0.0938.

Table 21 shows the total and monthly instantaneous rates of growth and mortality for 3- and 4-fresh-water Karluk sockye during each ocean year of life for each population model. Estimates

TABLE 21.—*Estimated instantaneous rates of growth and mortality and changes in bulk of 3- and 4-fresh-water Karluk River sockeye during each year of ocean life, population models 1, 2, 3, and 4*

[Mortality rate data from tables 5, 9, 13, and 17; growth rate data from table 20, adjusted for duration of ocean year (see text)]

Population model	Fresh-water age group	Ocean year	Duration of ocean year	Instantaneous rates of growth and mortality						Changes in bulk [1]	
				Yearly basis			Monthly basis			Per ocean year	Per month
				Growth	Mortality	Difference	Growth	Mortality	Difference		
			Months							*Percent*	*Percent*
1	3	1	14.17	3.0612	0.6320	2.4292	0.2160	0.0446	0.1714	1,035.0	18.7
		2	11.16	1.0465	.4977	.5488	.0938	.0446	.0492	73.1	5.0
		3	10.67	.7689	.4759	.2930	.0721	.0446	.0275	34.0	2.8
		4	11.83	.4278	.5276	−.0998	.0362	.0446	−.0084	−9.5	−0.8
	4	1	15.00	2.8745	.5790	2.2955	.1916	.0386	.1530	893.0	16.5
		2	11.67	.8897	.4505	.4392	.0762	.0386	.0376	53.6	3.8
		3	9.50	.5972	.3667	.2305	.0629	.0386	.0243	25.9	2.5
		4	12.00	.3820	.4632	−.0812	.0318	.0386	−.0068	−7.8	−0.7
2	3	1	14.17	3.0609	.7929	2.2680	.2160	.0560	.1600	866.0	17.4
		2	11.16	1.0584	.4326	.6258	.0948	.0388	.0560	87.0	5.8
		3	10.67	.7697	.2560	.5137	.0721	.0240	.0481	67.1	4.9
		4	11.83	.4278	.1028	.3250	.0362	.0087	.0275	38.4	2.8
	4	1	15.00	2.8820	.7038	2.1782	.1921	.0469	.1452	783.0	15.6
		2	11.67	.8917	.3701	.5216	.0764	.0317	.0447	68.5	4.6
		3	9.50	.5980	.1867	.4113	.0629	.0196	.0433	50.9	4.4
		4	12.00	.3820	.0888	.2932	.0318	.0074	.0244	34.1	2.5
3	3	1	14.17	3.0620	1.0842	1.9778	.2161	.0765	.1396	622.7	15.0
		2	11.16	1.0627	.1696	.8931	.0952	.0152	.0800	144.3	8.3
		3	10.67	.7695	.1622	.6073	.0721	.0152	.0569	83.5	5.8
		4	11.83	.4278	.1798	.2480	.0362	.0152	.0210	28.1	2.1
	4	1	15.00	2.8871	.9279	1.9592	.1925	.0619	.1306	609.4	13.9
		2	11.67	.8921	.1505	.7416	.0764	.0129	.0635	109.9	6.6
		3	9.50	.5980	.1226	.4754	.0629	.0129	.0500	60.9	5.1
		4	12.00	.3820	.1548	.2272	.0318	.0129	.0189	25.5	1.9
4	3	1	14.17	3.0620	.9599	2.1021	.2161	.0677	.1484	718.3	16.0
		2	11.16	1.0579	.2589	.7990	.0948	.0232	.0716	122.3	7.4
		3	10.67	.7693	.2475	.5218	.0721	.0232	.0489	68.5	5.0
		4	11.83	.4278	.2745	.1533	.0362	.0232	.0130	16.6	1.3
	4	1	15.00	2.8818	.7894	2.0924	.1921	.0526	.1395	710.4	15.0
		2	11.67	.8912	.2707	.6205	.0764	.0232	.0532	86.0	5.5
		3	9.50	.5976	.2204	.3772	.0629	.0232	.0397	45.8	4.0
		4	12.00	.3820	.2784	.1036	.0318	.0232	.0086	10.9	.9

[1] Exponential of difference between growth and mortality, less 1.

of the changes in bulk of sockye during ocean life are also given.

Under Population Model 1, the estimated natural mortality rates for 3- and 4-fresh-water sockeye are less than the estimated growth rates during each of the first 3 years of ocean life. The bulk (poundage) of 3-fresh-water fish is estimated to increase by 1,035, 73 and 34 percent, respectively, during the first, second, and third ocean years. The bulk of 4-fresh-water fish is estimated to increase by 893, 54 and 26 percent, respectively, during their first, second, and third years of ocean residence.

The estimated natural mortality rates during the fourth year of ocean life for the very small proportions of Karluk sockeye that mature as 4-ocean fish exceed the estimated growth rates. Hence, under the first population model, the bulk of Karluk sockeye in their fourth year at sea is estimated to decrease by about 10 percent (3-fresh-water fish) or 8 percent (4-fresh-water fish).

In the second model, the estimated ocean mortality rates for both fresh-water age groups are exceeded by the estimated growth rates throughout ocean life. During the first, second, third, and fourth ocean years, the bulk of 3-fresh-water sockeye is estimated to increase by 866, 87, 67, and 38 percent, respectively. Corresponding estimated increases for 4-fresh-water sockeye are 783, 69, 51, and 34 percent, respectively.

Under Population Model 3, the bulk of 3- and 4-fresh-water Karluk sockeye is estimated to increase in each year of ocean life. Estimated percentage increases in bulk during the first, second, third, and fourth years of ocean life are 623, 144, 84, and 28, respectively, for 3-fresh-water fish, and 609, 110, 61, and 26, respectively, for 4-fresh-water fish.

In the fourth population model also, the estimated natural mortality rates of 3- and 4-fresh-water fish are exceeded by the estimated growth rates in each ocean year. The bulk of 3-fresh-water sockeye is estimated to increase by 718, 122, 69, and 17 percent, respectively, during the first, second, third, and fourth years of ocean life. Increases in bulk of 4-fresh-water fish are estimated to be 710, 86, 46, and 11 percent, respectively, for the first through the fourth ocean years.

The percentage changes in bulk in table 21 show that, except for the relatively scarce 4-ocean fish under the first population model, any capture of Karluk sockeye before the end of their ocean life causes a loss of potential poundage yield, provided there exists an inshore fishery capable of catching the fish not needed for reproduction of the stock. The extent of the loss depends upon the distribution of ocean mortality and the year of ocean life in which the salmon would be captured by a high seas fishery. Computations of losses are not given here. It can be pointed out, however, that any mortality caused by net injury or inadvertent capture of Karluk sockeye during their first year of ocean life would result in an especially great loss of potential catch.

Attention is called to two matters relating to the estimated changes in bulk of Karluk sockeye during their ocean life. One, the estimates of net increase in bulk in table 21 are generally minimal due to the fact that the weighted average growth rates do not include the rapid growth that takes place during the last few months of ocean life of maturing sockeye. Secondly, if the distribution of ocean mortality is altered to reflect an increase in the mortality of maturing sockeye during their last month or two of ocean life, the bulk of the nonmaturing sockeye, as well as the loss in yield resulting from the capture of such fish, must also increase, because the total ocean mortality is fixed.

SUMMARY

Four population models simulating different temporal distributions of natural mortality during the ocean life of Karluk River sockeye salmon are developed. Assumptions employed in each of the models are discussed. Data collected in the late 1920's and early 1930's on the releases and returns of marked fish are used to estimate ocean mortality rates and maturity schedules of different fresh-water age groups of Karluk sockeye. The estimates primarily concern 3- and 4-fresh-water fish, the two fresh-water age groups that generally account for 95 percent or more of the annual runs to the Karluk system. The ocean mortality rate estimates are compared with available growth rate data to determine the changes in bulk (net increase or decrease in weight) of Karluk sockeye during ocean life.

In the first population model, natural mortality is assumed to be constant throughout ocean life. The estimates of monthly instantaneous ocean mortality rates obtained in this model generally decrease as the age and size of smolts increase: 0.0496 for 2-fresh-water smolts averaging 108 millimeters in length; 0.0446 for 3-fresh-water smolts averaging 131 millimeters in length; 0.0386 for 4-fresh-water smolts averaging 143 millimeters in length; and 0.0402 for 5-fresh-water smolts averaging 146 millimeters in length. These monthly instantaneous rates generate annual (12-month) ocean mortality rates of 44.8, 41.4, 37.1, and 38.3 percent, respectively.

Approximately 1.3, 51.4, 45.8, and 1.5 percent of the 3-fresh-water smolts are estimated to mature as 1-, 2-, 3-, and 4-ocean sockeye respectively. Corresponding percentages for 4-fresh-water smolts are about 3.3, 71.0, 24.6, and 1.0 percent.

The estimated natural mortality rates during the first 3 years of ocean life are less than the estimated ocean growth rates for both the 3-, and 4-fresh-water age groups of Karluk sockeye. During successive periods (called ocean years) of about 14, 11, and 11 months of ocean life, the bulk (poundage) of 3-fresh-water sockeye is estimated to increase by 1,035, 73, and 34 percent, respectively. During their first, second, and third ocean years (corresponding to periods of about 15, 12, and 10 months), 4-fresh-water sockeye are estimated to increase in bulk by 893, 54, and 26 percent, respectively.

The estimated natural mortality rates during the fourth year of ocean life for the very small proportions of 3- and 4-fresh-water fish that mature as 4-ocean fish exceed the estimated growth rates. Hence, under the first population model, the bulk of Karluk sockeye in their fourth year at sea is estimated to decrease by about 10 percent for 3-fresh-water fish and about 8 percent for 4-fresh-water fish.

In the second population model, the instantaneous natural mortality rate is assumed to be greatest in the first month of ocean life and then lecreases arithmetically in each of the following 47 or 48 months until it becomes zero. The first-nonth instantaneous mortality rates are estimated o be 0.0649 for 3-fresh-water sockeye and 0.0549 or 4-fresh-water sockeye. The instantaneous ates are estimated to decrease each month by bout 0.0014 for 3-fresh-water fish and 0.0011 for 4-fresh-water fish.

The natural mortality rates during the first, econd, third, and fourth ocean years for 3-fresh-vater fish are 54.7, 35.1, 22.6, and 9.8 percent, espectively. Corresponding estimates for 4-fresh-vater fish are 50.5, 30.9, 17.0, and 8.5 percent.

Under the second population model, about 1.6, 57.7, 39.8 and 0.8 percent of the 3-fresh-water molts are estimated to mature as 1-, 2-, 3-, and 4-ocean sockeye, respectively. Corresponding per-centages for the 4-fresh-water smolts are about 3.9, 74.5, 21.1, and 0.5.

For both the 3- and 4- fresh-water age groups, he estimated ocean mortality rates are exceeded y the estimated growth rates throughout ocean ife. During the first, second, third, and fourth cean years, the bulk of 3-fresh-water sockeye is stimated to increase by 866, 87, 67, and 38 ercent, respectively, while the bulk of 4-fresh-vater sockeye is estimated to increase by 783, 68, 51, and 34 percent, respectively.

In the third population model, the monthly nstantaneous natural mortality rate is assumed o be greatest during the first month of ocean life, lecreases geometrically by a factor of 0.5 in each f the next 5 months, and remains constant during he sixth and each succeeding month. First-nonth instantaneous mortality rates are estimated o be 0.4876 for 3-fresh-water sockeye and 0.4123 or 4-fresh-water sockeye. The instantaneous nortality rates in the sixth and each succeeding nonth are estimated to be 0.0152 for 3-fresh-water ish and 0.0129 for 4-fresh-water fish.

The natural mortality rates for 3-fresh-water ish during their first ocean year (approximately 4 months) is estimated to be 66.2 percent. The ate for succeeding 12-month periods is estimated o be 16.7 percent. The natural mortality rate or 4-fresh-water fish during their first ocean year 15 months) is estimated to be 60.5 percent. The ate for succeeding 12-month periods is estimated o be 14.3 percent.

About 2.4, 59.8, 37.0, and 0.8 percent of the 3-fresh-water smolts are estimated to mature as 1-, 2-, 3-, and 4-ocean sockeye, respectively, under the third population model. Corresponding estimates for the 4-fresh-water smolts are 5.2, 74.8, 19.6, and 0.5 percent.

The estimated natural mortality rates of 3- and 4-fresh-water fish are less than the estimated growth rates during each ocean year. The bulk of 3-fresh-water sockeye is estimated to increase by 623, 144, 84, and 28 percent during the first, second, third, and fourth ocean years, respectively. Corresponding estimates of percentage increases in bulk of 4-fresh-water fish are 609, 110, 61, and 26.

In the fourth population model, the instantaneous natural mortality rate is assumed to be greater for 3-fresh-water sockeye than for 4-fresh-water fish during the first month of ocean life, greater for both fresh-water age groups during the first month than during the second and succeeding months, and constant and the same for the two fresh-water age groups during each month of ocean residence following the first month.

Starting with the assumption that the first-month instantaneous ocean mortality rate of 4-fresh-water sockeye is 20 times the mortality rate of this fresh-water age group in each of the following months, the instantaneous mortality rates of sockeye of that fresh-water age group are estimated to be 0.4646 during the first month of ocean life and 0.0232 during each succeeding month. Under this model, 0.0232 is also the estimated monthly instantaneous natural mortality rate of 3-fresh-water sockeye after their first month in the ocean. The first-month instantaneous mortality rate of 3-fresh-water fish is estimated to be 0.6544, about 40 percent greater than the corresponding estimate for 4-fresh-water fish and about 28 times the mortality rate of 3-fresh-water fish during the second and succeeding months of ocean life.

The total ocean mortality rate for 3-fresh-water fish during their first ocean year is estimated to be 61.7 percent. The corresponding estimate for 4-fresh-water sockeye is 54.6 percent. For both fresh-water age groups the rate for succeeding 12-month periods is estimated to be 24.3 percent.

The maturity schedules of 3- and 4-fresh-water smolts are estimated to be about the same in the fourth population model as in the second model.

The estimated natural mortality rates of 3- and

4-fresh-water sockeye are exceeded by the estimated growth rates in each ocean year. The bulk of 3-fresh-water sockeye is estimated to increase by 718, 122, 68, and 17 percent, respectively, during the first, second, third and fourth years of ocean life. Corresponding estimates of increases in bulk of 4-fresh-water fish are 710, 86, 46, and 11 percent.

The estimated percentage changes in bulk show that, except for the relatively scarce 4-ocean fish under the first population model, any capture of Karluk sockeye before the end of their ocean life causes a loss of potential yield, provided there exists a coastal fishery capable of catching the fish not needed for reproduction of the stock.

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LITERATURE CITED

Barnaby, Joseph T.

1932. The growth of the red salmon (*Oncorhynchus nerka* Walbaum) of the Karluk River and the growth of its scales. M.A. Thesis, Stanford University, 50 p.

1944. Fluctuations in abundance of red salmon *Oncorhynchus nerka* (Walbaum) of the Karluk River, Alaska. U.S. Fish and Wildlife Service, Fishery Bulletin 39, vol. 50, pp. 237–295.

Bevan, Donald Edward

1962. Estimation by tagging of the size of migratin salmon populations in coastal waters. *In* Studie of Alaska red salmon, edited by Ted S. Y. Kov University of Washington (Seattle), Publications in Fisheries, new series, vol. 1, pp. 373–449. 34 figs

Foerster, R. E.

1934. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka* at Cultus Lake, British Columbia. No. 4. Th life history cycle of the 1925 year class with natura propagation. Contributions to Canadian Biology and Fisheries, N.S., vol. 8, No. 27, pp. 345–355.

1936. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. No. 5. Th life history cycle of the 1926 year class with artificial propagation involving the liberation of free-swimming fry. Journal of the Biological Board o Canada, vol. 2, No. 3, pp. 311–333.

1937. The return from the sea of sockeye salmon (*Oncorhynchus nerka*) with special reference to percentage survival, sex proportions and progress o migration. Journal of the Biological Board o Canada, vol. 3, No. 1, pp. 26–42.

Parker, Robert R.

1962. Estimations of ocean mortality rates for Pacific salmon (*Oncorhynchus*). Journal of the Fisheries Research Board of Canada, vol. 19, No. 4 pp. 561–589.

Rich, Willis H., and Frederick G. Morton

1929. Salmon tagging experiments in Alaska, 1927 and 1928. Bulletin of the U.S. Bureau of Fisheries, 1929 (1930), vol. 45 (Doc. 1057; issued October 12, 1929), pp. 1–23.

Ricker, W. E.

1962. Comparisons of ocean growth and mortality of sockeye salmon during their last two years. Journal of the Fisheries Research Board of Canada, vol. 19, No. 4, pp. 531–560.

Rounsefell, George A.

1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. U.S. Fish and Wildlife Service, Fishery Bulletin 130, vol. 58, pp. 83–169.

A METHOD OF MEASURING MORTALITY OF PINK SALMON EGGS AND LARVAE

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ABSTRACT

A method of estimating total mortality of salmon eggs and larvae from time of spawning to time of sampling is described. The method provides a measure of mortality, regardless of cause, and is unaffected by the disappearance of dead eggs or larvae.

Total mortality rate is calculated from estimates of abundance and fecundity of parent female spawners (potential egg deposition) and abundance of live eggs and larvae in spawning beds at the time of sampling. A hydraulic sampler, developed to collect samples of eggs and larvae, is described.

Two sources of bias are considered in mortality rates calculated from percentages of dead eggs and larvae in samples: (1) eggs not initially buried by spawners, and (2) eggs and larvae disappearing from the spawning bed. Neither source of bias exists where mortality is calculated from estimated potential egg deposition and abundance of live eggs and larvae at time of sampling.

The efficiency of estimating abundance of eggs and larvae is affected by their tendency to be clustered. Clustering causes the sample variance to increase with the sample mean, and confidence limits of estimates of abundance may be widely separated. The use of a logarithmic transformation improved the efficiency of estimates in certain instances.

A chi-square test based on the premise that a change in the total mortality level would be associated with a change in frequency of occurrence of dead or live eggs and larvae in samples is described. This test was useful in identifying periods when significant mortality occurred, especially where confidence limits of total mortality percentages were widely separated.

Pink salmon (*Oncorhynchus gorbuscha*) is the most abundant of the Pacific salmons and in most years provide a larger commercial catch than all other salmon species. In the eastern Pacific, pink salmon are commercially important from Bristol Bay, Alaska, to Puget Sound, Washington. They support a major fishery in southeastern Alaska where there are about 1,100 spawning streams (Martin, 1959).

Spawning female pink salmon bury their eggs n gravel beds of coastal streams and die soon fter spawning. Their eggs are deposited in ummer or autumn and hatch within 60 to 90 days. The larvae usually remain in the streambed over winter and the fry emerge and migrate immediately to salt water the following spring. In most instances fry do not feed in fresh water.

There is evidence that fry production is ultimately limited by the area available for spawning. Ricker (1954) and Neave (1958) note that escapements of large numbers of spawners do not necessarily result in large yields of fry. Their findings indicate that the yield of fry approaches an asymptote (and may even decline at high spawning densities) with increased density of spawners. Ricker points out that optimum escapement would most likely occur at a level intermediate between low and high density of spawners.

Determining optimum escapement will depend

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ultimately on a thorough understanding of factors limiting fry production. Total fresh-water mortality of pink salmon has been measured in McClinton, Hook Nose, and Morrison Creeks, British Columbia (Pritchard, 1948; Neave, 1953; Hunter, 1959) and in Sashin Creek, southeastern Alaska (Davidson and Hutchinson, 1942; Hutchinson and Shuman, 1942; Merrell, 1962). Mortalities in those streams ranged from 76 to over 99 percent.

Periods in the fresh-water life of pink salmon during which major mortalities occur have not yet been sufficiently elucidated. Variable mortalities occur among adults before spawning, among eggs and larvae, and among fry. The period beginning with egg deposition and terminating with emergence of fry typically encompasses 80 to 90 percent of the total fresh-water life of pink salmon, and during most of this period the developing embryos and larvae are immobilized and concealed by the surrounding solids of the streambed. While buried in the streambed, eggs and larvae are subjected to numerous stresses imposed by the environment that may cause death.

The measurement of mortality in spawning beds is complicated in many instances by the disappearance of eggs and larvae from decomposition, scavenging, predation, and bed movement. Where disappearance of eggs and larvae has taken place, the percentages of dead eggs and larvae collected in samples will underestimate the true total mortality percentage. There is a need, then, to devise methods of estimating changes in density of eggs and larvae in spawning beds so that estimates of total mortality can be calculated. This paper describes procedures that can be employed to measure total mortality percentage of pink salmon eggs and larvae from egg deposition to any selected time during the period of streambed residence.

Studies on environmental factors causing mortality of pink salmon eggs and larvae were initiated by the Fisheries Research Institute, University of Washington, in 1948. These early studies were undertaken in streams near Ketchikan, Alaska, with financial support from the Alaska salmon industry. Industry-supported studies were discontinued after 1955, and in 1956 Saltonstall-Kennedy Act funds were provided by the Bureau of Commercial Fisheries to study the effects o logging on pink salmon. Mortality studies were continued as part of this program. The study streams were Harris River and Indian and Twelve mile Creeks, located on Prince of Wales Island about 40 miles west of Ketchikan.

Three important problems were considered in the development of methods used to measure periodically egg and larval mortality. First equipment and methods for obtaining samples o eggs and larvae representative of the population sampled were developed and tested. Second equations for calculating total mortality percentage from the time of spawning to the time o sampling were formulated. Third, statistica methods to test for significant changes in tota mortality percentage were tried.

COLLECTING EGGS AND LARVAE

Several workers have examined samples of eggs and larvae collected from spawning beds and have calculated the mortality percentage from the proportion of dead eggs and larvae in samples (Hobbs, 1937 and 1940; Cameron, 1940; Briggs, 1953; Hatch, 1957; Hunter, 1959; Mathisen, 1962) This method introduces bias into calculated tota mortality percentages if parent females have failed to deposit eggs or eggs and larvae have disappeared from the spawning bed. To overcome these sources of bias, periodic estimates of abundance of eggs and larvae must be obtained. A method for calculating total mortality percentage from estimated density of live eggs and larvae was used.

Density of eggs and larvae in the spawning bed was estimated by collecting specimens from small discrete quadrats or circular plots (sampling units) ranging from 2 to 4 square feet in area. An estimate of the average number of eggs and larvae per square foot of spawning bed was obtained by sampling a number of units located randomly within a spawning bed. The accuracy of this estimate was influenced largely by the thoroughness with which eggs and larvae were collected from within a sampling unit without losing any, yet excluding eggs and larvae adjacent to the sampling unit. To meet the requirements of the sampling scheme special equipment for collecting eggs and larvae was developed. The apparatus, called a hydraulic sampler, was first tried in 1956.

DESCRIPTION OF THE HYDRAULIC SAMPLER

The hydraulic sampler utilizes suction created by passing water at high velocity through an annular aperture to mix air with water. The air and water mixture is injected into the streambed to free eggs and larvae from bottom materials. The device is patterned after equipment used by Mathisen (1962). The major difference is that Mathisen excavated both gravel and eggs with the suction created.

Basic components of the hydraulic sampler are a 7,200-gallon per hour centrifugal water pump and a cone assembly that creates a mixture of air and water. Water is delivered by the pump to the cone through flexible rubber hose of 1½-inch diameter. The mixture of air and water from the cone assembly is injected into the streambed through a nozzle (fig. 1).

A jacket between the terminal openings of the cone assembly receives water from the pump which is forced under pressure from the jacket at high speed through an annular aperture on the inside of the tube. Water flowing through the aperture creates a suction at the opening opposite the direction of flow, and water and air mix beyond the aperture as they flow toward the nozzle. The size of the aperture can be adjusted to regulate the quantity of air in the mixture. A disassembled cone is shown in figure 2. Drawings of the cone assembly are shown in figure 3.

OPERATION OF THE HYDRAULIC SAMPLER

Eggs and larvae were flushed from the streambed by rising air bubbles and water currents and were collected in a net attached to the downstream side of a metal frame outlining the sampling unit (fig. 4). Square frames enclosing 4 square eet and circular frames enclosing 2 square feet were tried. The circular frame is recommended because it has the smallest perimeter for a given area, which minimizes the number of eggs and arvae removed from outside the boundary of the sampling unit and not collected.

Penetration of the nozzle into the streambed was greatly facilitated by the flow of water and ir from the nozzle. The depth of penetration depended largely upon size composition of bottom materials, being least where large cobbles were present. In mixtures of fine gravel and sand it was possible to penetrate readily more than 24 nches.

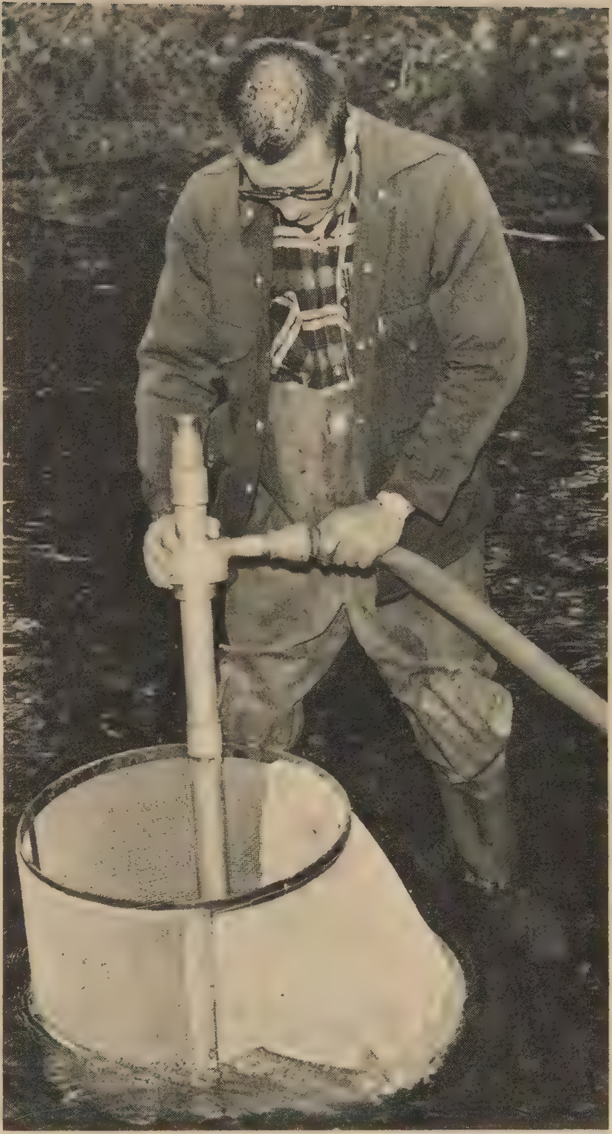

FIGURE 1.—Collecting pink salmon eggs or larvae with hydraulic sampler.

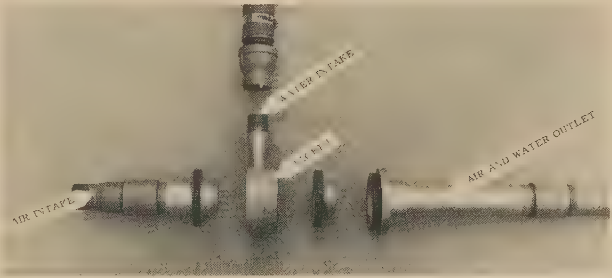

FIGURE 2.—Disassembled cone assembly of hydraulic sampler.

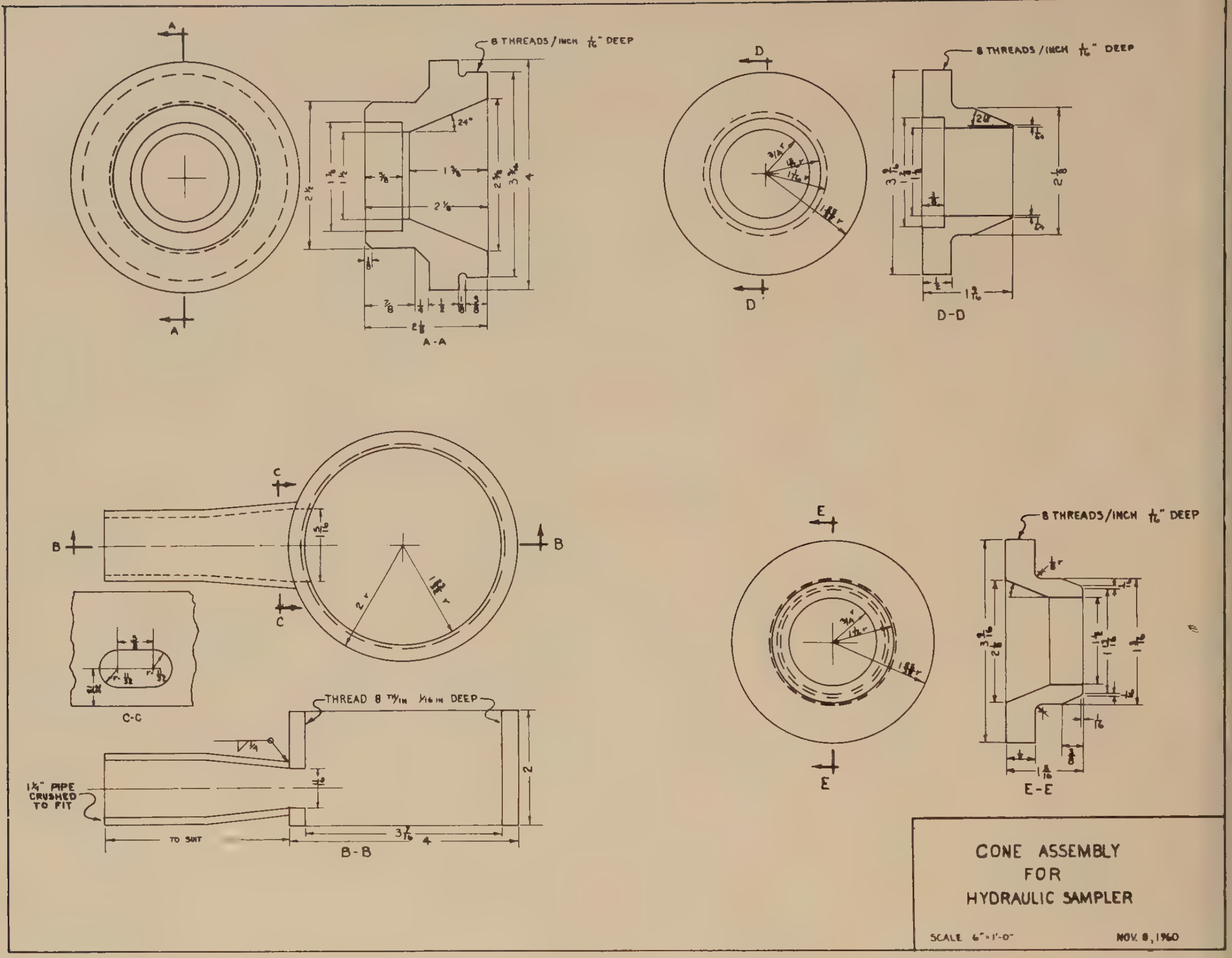

FIGURE 3.—Machine drawing of cone assembly of hydraulic sampler.

In this study, each sampling unit was sampled by two persons. As soon as the first person felt he had removed all eggs and larvae from within a sampling unit, the second person attempted to remove any that might have been missed.

PERFORMANCE OF THE HYDRAULIC SAMPLER

When a streambed is excavated with a shovel, it is difficult to collect eggs and larvae from one sampling unit without collecting specimens from adjacent units. Difficulties occur because stream bottom materials containing eggs and larvae shift horizontally when a hole is dug. With the hydraulic sampler, heavier materials were not transported away, and very little horizontal shift of the streambed occurred. Furthermore, the action of air and water currents was restricted to an area adjacent to the nozzle orifice, and the disturbance of the streambed beyond the boundaries of the sampling unit was minimized.

The percentage of eggs and larvae recovered from a sampling unit with the hydraulic sampler was estimated from results of two tests. First, after completion of the initial sampling by two persons, sampling units were resampled by a third person in an attempt to remove additional specimens. In the opinion of those doing the work, sufficient effort was expended in resampling to remove virtually all specimens within the boundaries of sampling units. In tests of this type, the two persons doing the initial sampling were not advised that the resampling was to be done. Second, known numbers of preserved eggs were buried. The persons doing the sampling were not advised either of the number or of the exact location of preserved eggs buried within a

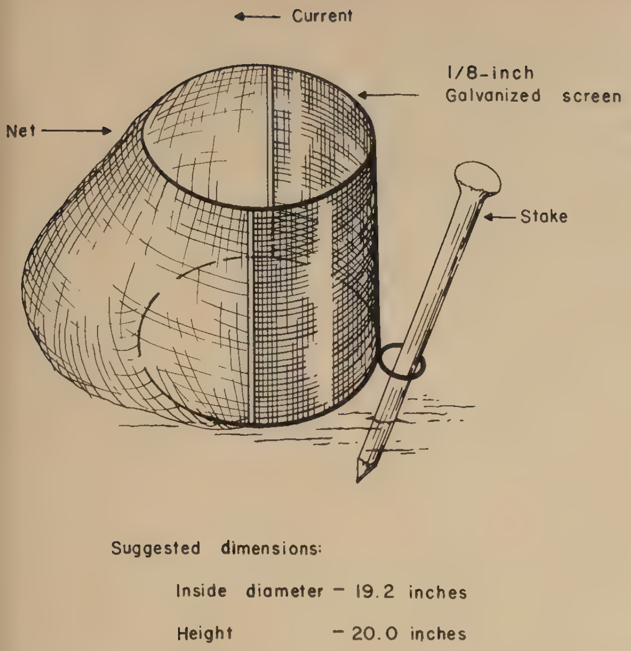

FIGURE 4.—Circular frame and collection net used with hydraulic sampler.

sampling unit. In tests of this type, no resampling was done to recover eggs not recovered by two persons sampling.

The mean percentage of eggs recovered after two persons had sampled was about the same for both types of tests—93 percent. Results of tests where the initial effort by two persons was followed by resampling by a third person are given in table 1. Table 2 gives results of tests where known numbers of preserved eggs were buried and recovered by two persons sampling.

TABLE 1.—*Number and percentage of naturally spawned eggs collected by two persons sampling followed by resampling*

Collected by two persons sampling	Collected by a third person resampling	Collected by two persons sampling
Number	*Number*	*Percent*
30	5	85.7
327		100.0
108	7	93.9
85	1	98.8
249	5	98.0
235	126	65.1
634	12	98.1
521	35	93.7
45		100.0
203	6	97.1
Mean		93.0
Standard deviation		10.7

To estimate the density of salmon eggs and larvae in a spawning bed, a recovery percentage of 90 percent was assumed. Furthermore, because a high percentage of eggs present in the test sampling units was collected, it was concluded that the possibility of introducing significant bias to estimates of abundance through an error in the assumed recovery percentage was minimized.

BROKEN SHELLS

Hobbs (1937), Cameron (1940), and Mathisen (1962) noted the presence of clean broken shells among eggs recovered from the gravel. The shells apparently originated from eggs damaged during excavation. Each author eliminated clean broken shells from his analysis because it was not possible to determine if these eggs were dead or alive when damaged.

TABLE 2.—*Number and percentage of buried preserved eggs collected by two persons sampling*

Buried	Recovered by two persons sampling	Recovered by two persons sampling
Number	*Number*	*Percent*
200	175	87.5
200	195	97.5
200	174	87.0
200	183	91.5
582	552	94.8
10	10	100.0
50	50	100.0
150	129	86.0
200	171	85.5
200	191	95.5
173	159	91.9
80	77	96.2
140	136	97.1
19	17	89.5
380	354	93.2
40	39	97.5
200	194	97.0
60	57	95.0
120	116	96.7
100	83	83.0
Mean		93.1
Standard deviation		5.1

We found that fewer eggs were broken by the hydraulic sampler than by a shovel. Comparisons were made between eggs collected by the two methods on Indian Creek in November 1956 (table 3). Observations were given equal weight for this comparison. Since clean broken shells averaged only 0.24 percent of the total eggs per sample, they are not included in our mortality estimates.

MEASURING MORTALITY

The percentage of eggs and larvae dying from the time of spawning to the time of sampling can be calculated from estimates of potential egg deposition and abundance of live eggs and larvae in the spawning bed at the time of sampling. It will be shown how total mortality percentage calculated in this manner is unbiased either by failure of females to deposit or bury their eggs or by disappearance of eggs and larvae from the spawning bed. Eggs that are not deposited may be retained in the coelom of the female and, may be consumed by predators, or may drift free of the spawning bed. Factors causing eggs and larvae to disappear include consumption by predators or scavengers, decomposition, superimposition of redds, and erosion of spawning beds by floods, ice, or debris.

TABLE 3.—*Number and percentage of broken shells in samples collected with a shovel compared with those collected with the hydraulic sampler, Indian Creek, November 1956*

Shovel			Hydraulic sampler		
Collected	Broken	Broken	Collected	Broken	Broken
Number	*Number*	*Percent*	*Number*	*Number*	*Percent*
276	6	2.17	115	1	0.87
260	15	5.77	608	------	------
585	8	1.37	368	------	------
493	16	3.25	128	------	------
24	------	------	779	3	.39
602	5	.83	447	------	------
329	2	.61	149	------	------
223	1	.45	13	------	------
157	3	1.91	221	1	.45
240	4	1.67	445	4	.90
372	4	1.08	2,105	4	.19
723	27	3.73	893	1	.11
438	16	3.65	872	------	------
679	7	1.03	1,125	11	.98
773	3	.39	341	2	.59
521	12	2.30	103	------	------
------	------	------	234	------	------
------	------	------	295	------	------
------	------	------	1,080	1	.09
Mean	------	1.89	------	------	.24

The notations listed below will be used in the discussions that follow:

D=Actual number of dead eggs and larvae in a spawning bed at time of sampling.
A=Actual number of live eggs and larvae in a spawning bed at time of sampling.
$P=D+A$.
E=Potential number of eggs available for deposition in a spawning bed.
x=Fraction of E surviving to time of sampling.
y=Fraction of E not deposited in the spawning bed or lost from the spawning bed prior to sampling.
$1 \geq x+y$.
M_r=Mortality percentage calculated from the proportions of dead eggs and larvae collected in samples.
M_t=Calculated total mortality percentage from time of spawning to time of sampling.

BIAS IN CALCULATED MORTALITY LEVELS

An estimate of mortality level commonly reported in the literature is the ratio of number of dead to total number of eggs and larvae collected in k samples from a spawning bed, i.e.

$$M_r=\frac{1}{k}\left(\sum_{i=1}^{k}\left(\frac{\text{live}}{\text{live}+\text{dead}}\right)_i\right) \tag{1}$$

If it is assumed that live and dead eggs and larvae are collected in the same ratio as they occur in the total population, then the expected value of M_r is

$$\frac{D}{P}=1-\frac{A}{P} \tag{2}$$

Substituting

$$P=E-yE \text{ and}$$
$$A=xE$$

gives

$$M_r=1-\frac{x}{1-y} \tag{3}$$

where y is the bias introduced by disappearance of eggs and larvae and by failure of eggs to be deposited.

An estimate of total mortality level (M_t) which is not biased by y may be obtained from estimates of the actual population of live eggs and larvae in the spawning bed (A) and the potential egg deposition (E) in the following manner:

$$M_t=1-\frac{A}{E}=1-x \tag{4}$$

If all eggs are deposited in the spawning bed, and if there are no subsequent losses of eggs or larvae from the spawning bed, the value of y in equation (3) is zero; and equations (3) and (4) are identical. In this case, the observer can calculate the total mortality percentage by the two methods and select the one that is most efficient.

The calculation of total mortality level (M_t) based on E and A, equation (4), requires estimates of potential egg deposition and the number of live specimens in the spawning area at the time of sampling. Consideration will be given to certain important problems in obtaining estimates of E and A, but considerable additional research will be required before the methods of estimating mortality described in this paper become fully developed.

ESTIMATION OF POTENTIAL EGG DEPOSITION

An estimate of potential egg deposition can best be obtained from weir counts, but in some instances it may be desirable or necessary to estimate numbers of females spawning within defined stream sections or in streams where the construction of a weir is not feasible. The present study was conducted in intertidal spawning beds, making it impractical to construct weirs. The number of female salmon spawning in a study area was determined from observation. The method is illustrated for Harris River in 1959 as follows:

Daily counts of the number of female pink salmon spawning in the sampling area were obtained (fig. 5). Daily observations were made of 43 tagged pink salmon females to obtain an estimate of the average time each spawning female occupied the spawning ground. In 1959, tagged female pink salmon occupied the spawning bed an average of 10.35 days (range: 4 to 20 days), and it was assumed that untagged females occupied the spawning bed an equal time. To estimate the total number of females spawning within the sampling area, the area under the curve (fig. 5) was divided by the average number of days each female occupied the spawning bed. The estimate was

$$\frac{15{,}850 \text{ female-days}}{10.35 \text{ days}}=1{,}531 \text{ female pink salmon.}$$

The average fecundity of pink salmon that spawned in McClinton Creek, northern British Columbia (Foerster and Pritchard, 1941), was used as an estimate of fecundity, since adequate data on fecundity of Harris River pink salmon were not available. For the years 1930–40, McClinton Creek pink salmon averaged 1,733 eggs per female. An average of 1,700 eggs per Harris River female was assumed. The potential egg deposition (E) within the Harris River sampling area in 1959 was thus estimated to be

$$1{,}531\times1{,}700=2.6 \text{ million.}$$

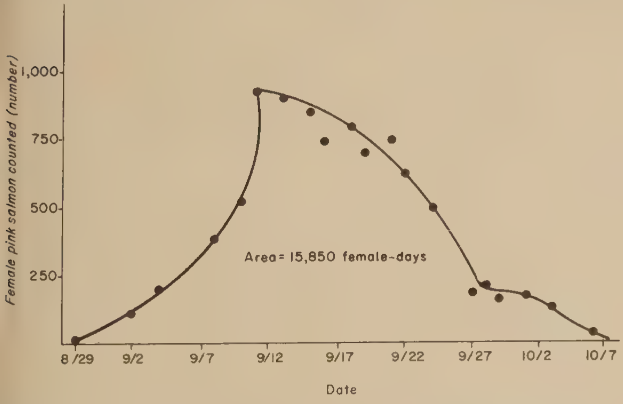

FIGURE 5.—Number of female pink salmon counted within the Harris River sampling area in 1959.

The use of tagged females to obtain estimates of the average time female pink salmon occupied the spawning bed involved the assumption that tagged females lost no tags. It was assumed also that they behaved in a manner similar to and suffered the same mortality as untagged females, that is, tagged and untagged females reacted the same while on the spawning bed.

Although no attempt was made to measure variance in estimates of potential egg deposition, it is a random variable subject to at least two sources of sampling variability—(1) the estimated number of females spawning and (2) their estimated average fecundity. In the future, studies should be undertaken to evaluate the variance in estimates of each statistic. It would be more satisfactory, however, to conduct mortality studies in streams equipped with weirs for enumeration of adults, making it possible to minimize such sources of variation.

CALCULATION OF TOTAL MORTALITY LEVEL

A confidence interval estimate of total mortality level is calculated from the double inequality.

$$1-\frac{\bar{a}}{E'}<M_t<1-\frac{\underline{a}}{E'} \qquad (5)$$

The values $\bar{a}$ and $\underline{a}$ are the upper and lower confidence limits of the estimated number of live eggs and larvae per square foot of spawning bed, and E' is the expected number per square foot. Values of $\bar{a}$ and $\underline{a}$ can be calculated with the t-distribution and the standard error of the mean obtained either from arithmetic counts of live eggs and larvae or from transformed values.

Double inequality (5) is derived in the following manner:

$$\text{Let survival to time } t=\frac{A_t}{E}=1-M_t. \qquad (6)$$

Let the confidence interval estimate of the number of live eggs and larvae per square foot within a sampling area be represented by the double inequality

$$\underline{a}<A_t<\bar{a} \qquad (7)$$

Dividing (7) by the potential egg deposition, E, gives

$$\frac{a}{E}<1-M_t<\frac{\bar{a}}{E} \tag{8}$$

which is equivalent to

$$1-\frac{\bar{a}}{E}<M_t<1-\frac{a}{E} \tag{9}$$

For calculating total mortality, the value E' is substituted for E in double inequality (9). E' is E adjusted to account for the percentage of specimens actually collected within a sampling unit. Tests to determine the percentage collected (tables 1 and 2) suggested that $E' \approx 9/10\ E$. This relationship was used to calculate values of E'.

The method of calculating M_t is illustrated with data from Harris River samples collected October 6, 1959. A 90-percent confidence interval estimate of mean number of live eggs per square foot was calculated from the arithmetic counts, giving the following estimate of their abundance:

$$16.0 \text{ eggs/sq. ft.} < A < 35.0 \text{ eggs/sq. ft.}$$

The expected number of eggs per square foot (E') was calculated from the estimated total potential egg deposition, the size of the sampling area (62,640 sq. ft.), and the estimated percentage recovered, i.e.,

$$E'=\left(\frac{9}{10}\right)\left(\frac{2{,}600{,}000 \text{ eggs}}{62{,}640 \text{ sq. ft.}}\right)=37.4 \text{ eggs/sq. ft.}$$

Using inequality (5) the estimated total mortality was

$$1-\frac{35.0}{37.4}<M_t<1-\frac{16.0}{37.4} \text{ or } 6.4\%<M_t<57.2\%.$$

The estimated mean mortality was 31.6 percent. For the same sample, M_r was estimated to be only 5 percent.

COMPARING SAMPLES FOR SIGNIFICANT DIFFERENCES

It is not always possible to determine by inspecting confidence limits alone if calculated mean total mortality levels (M_t) differ significantly. The use of confidence limits to detect significant differences implies that assumptions of analysis of variance are satisfied. Furthermore, it is difficult to assign exact levels of significance to confidence limits. This is due in part to the reduced efficiency of confidence-interval estimates of abundance calculated from arithmetic counts because the distribution of eggs and larvae within the streambed is nonrandom.

Arithmetic counts for calculating confidence-interval estimates of abundance are not always most efficient, but are not too likely to be seriously biased. It should be noted, however, that use of the t-distribution for setting confidence limits requires that sample means from a given population be normally distributed. This assumption can be satisfied for highly skewed population distributions if the sample size is large.

In the discussions that follow, the use of a logarithmic transformation to improve the efficiency of confidence-interval estimates of abundance will be considered. Also described are the uses of single binomial parameters and live-dead ratios to detect changes in total mortality level.

DISTRIBUTION OF EGGS AND LARVAE

The distribution of eggs and larvae within a spawning bed influences the choice of statistical methods to test for sufficient and significant differences among calculated total mortality percentages. Because spawning salmon deposit their eggs in egg pits, eggs are initially clustered. Furthermore, evidence from field sampling indicates that occurrence of mortality does not materially affect the tendency of surviving eggs and larvae to be clustered.

When organisms tend to become clustered, the variance commonly increases as their mean abundance increases. The observed relationship between the mean number of live eggs and larvae collected per square foot of spawning bed and the sample variance is given in table 4. Samples were collected in autumn and winter and were from populations suffering light to heavy mortality. The data from table 4 are plotted in figure 6 to show graphically the relation between mean and variance.

The negative binomial distribution has frequently been fitted to counts of organisms where mean and variance were directly related. Bliss (1953) described several models of the negative binomial. One was derived to describe insect larvae hatching from eggs laid in masses, a condition possibly similar to that found among salmonid eggs and larvae.

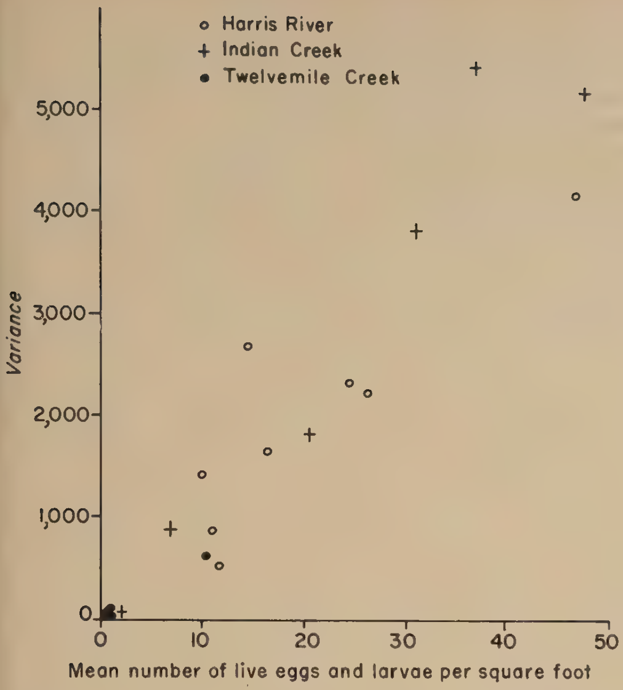

FIGURE 6.—Relation of mean to variance of live eggs and larvae collected per square foot of spawning bed in three southeastern Alaska streams.

TABLE 4.—*Means and variances of number of live eggs and larvae collected per square foot of spawning bed in three southeastern Alaska streams*

Stream and year class	Collection date	Size of sampling unit (sq.ft.) [1]	Number of sampling units	Mean	Variance	Variance mean
Harris River:						
1957	Apr. 1, 1958	4	74	1.1	41.2	37.5
1958	Sept. 18, 1958	4	34	10.7	878.9	82.1
1958	Nov. 15, 1958	4	32	14.6	2,688.8	184.2
1958	Apr. 5, 1959	4	66	9.9	1,408.7	142.3
1959	Oct. 6, 1959	4	74	24.6	2,338.1	95.0
1959	Oct. 20, 1959	4	43	26.2	2,229.3	85.1
1959	Nov. 16, 1959	4	20	16.3	1,633.0	100.2
1959	Feb. 26, 1960	4	69	11.4	512.2	44.9
1960	Sept. 27, 1960	2	56	47.2	4,157.5	88.1
Indian Creek:						
1958	Nov. 15, 1958	4	50	20.5	1,832.4	89.4
1958	Mar. 28, 1959	4	91	6.8	905.1	133.1
1959	Oct. 10, 1959	4	75	31.0	3,845.0	124.0
1959	Nov. 10, 1959	4	41	47.8	5,192.3	108.6
1959	Feb. 29, 1960	4	70	2.1	70.4	33.5
1960	Sept. 22, 1960	2	89	36.9	5,424.5	147.0
Twelvemile Creek:						
1958	Nov. 30, 1958	4	29	.4	4.2	10.5
1958	Dec. 28, 1958	4	32	.1	.1	1.0
1958	Mar. 24, 1959	4	47	.1	.5	5.0
1959	Oct. 27, 1959	4	77	1.0	68.3	68.3
1959	Feb. 21, 1960	4	56	.04	.07	1.8
1960	Sept. 30, 1960	2	50	10.3	636.1	61.8

[1] Sampling units of 4 square feet were quadrats and sampling units of 2 square feet were circles.

The negative binomial is a unimodal distribution; but biomodal or multimodal distributions may result also from contagion, as, for example Neyman's contagious distributions which have been studied with regard to their modality and other properties (Beall and Rescia, 1953; Beall, 1954). However, Beall (1954) concluded that, regardless of the form of the distribution, if contagion occurred the empirical relationship between population variance (θ^2) and mean (μ) was

$$\theta^2 = \mu + \beta\mu^2 \tag{10}$$

The β term in equation (10) is a constant. Its value depends upon the degree of contagion—with β increasing with increasing degree of contagion.

Curves of equation (10) are drawn in figure 7 for $\beta=3$ and $\beta=30$.

The variance and mean of samples of live eggs and larvae collected from Harris River are shown in figure 7 as open circles. The plotted points indicated that values of β associated with samples of live eggs and larvae collected in Harris River fell mostly between $\beta=3$ and $\beta=30$. Values of β were also calculated for the Harris River samples from the expected frequency of zero observations in a negative binomial distribution (see Anscombe, 1949, and Bliss, 1953) and values $\beta \geqq 2.9$ were obtained by this method for the samples plotted in figure 7.

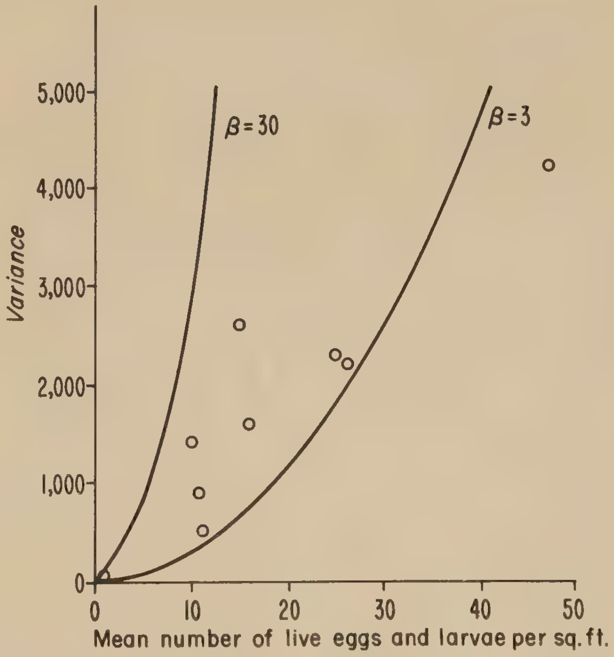

FIGURE 7.—Curves of $\theta^2=\mu+\beta\mu^2$ for $\beta=3$ and $\beta=30$. Values of variance and mean for samples collected in Harris River are plotted as open circles.

TRANSFORMATION OF COUNTS

A transformation was sought to render variance independent of the mean and to increase efficiency of confidence interval estimates of abundance. Where variance and mean are related according to equation (10), the arc hyperbolic sine transformation is appropriate; but for larger values of β, the transformed values vary almost as the log[1] of the number of live eggs and larvae in a sample (Beall, 1942). Furthermore, Barnes (1952) showed that the logarithmic was equally as applicable as the more complex arc hyperbolic sine transformation where values of β were large.

Jones (1956) and Taft (1960) used the logarithmic transformation to set confidence limits to estimates of abundance of bottom fish and sardine eggs because mean and variance were directly related. Since field sampling data suggested that the logarithmic transformation was also applicable for pink salmon eggs and larvae, the transformation

$$b_i=\log (n_i+\beta) \qquad (11)$$

was tried. In equation (11), n_i is the number of live eggs and larvae per square foot at the i^th^ point and b_i is the transformed variate. A value of β was calculated for each sample from the expected frequency of zero observations in a negative binomial distribution. The technique is described by Anscombe (1949) and Bliss (1953). It requires an iterative solution of the equation

$$\frac{1}{\beta} \log (1+\beta\bar{n})=\log \left(\frac{k}{k_o}\right), \qquad (12)$$

where k is the total number of observations (sampling units), k_0 is the number of zero observations, and $\bar{n}$ is the sample arithmetic mean.

For samples where $\beta>3.0$, the logarithmic transformation (equation 11) helped render the variance independent of the mean (see table 5) and improved the efficiency of confidence interval estimates (table 6). However, for samples where $\beta<3$, there was no apparent improvement in efficiency, and confidence-interval estimates had a significant bias when compared with the arithmetic mean (table 6).

TABLE 5.—*Comparison of mean and variance of untransformed and log-transformed counts of number of live eggs and larvae per square foot collected in Harris River samples where $\beta>3.0$*

Date of collection	Arithmetic values (N_i)		Log-transformed values ($b_i=\log (n_i+\beta)$)	
	Mean	Variance	Mean	Variance
1958				
Apr. 1	1.1	41.2	2.100	<0.001
Sept. 18	10.7	878.9	.985	.131
Nov. 15	14.6	2,688.8	1.479	.058
Dec. 20	3.7	193.6	1.185	.029
1959				
Apr. 5	9.9	1,408.7	1.576	.032
Oct. 6	24.6	2,338.1	1.057	.292
Oct. 20	26.2	2,229.3	1.130	.284
Nov. 16	16.3	1,633.0	.949	.231
1960				
Feb. 26	11.4	512.2	1.040	.143
1961				
Mar. 7	6.6	203.2	.909	.099

TABLE 6.—*Ninety-percent confidence interval estimates of mean number of live eggs and larvae per square foot in Harris River calculated from untransformed and log-transformed data*

Year class and collection date	Arithmetic mean	Confidence interval estimate of mean	
		Untransformed	Log-transformed
1957			
April 1, 1958	1.1	$0<\mu<2.3$	$0<\mu<2.2$
1958			
September 18, 1958	10.7	$2.1<\mu<19.3$	$4.5<\mu<11.2$
November 15, 1958	14.6	$0<\mu<30.1$	$4.8<\mu<16.6$
December 20, 1958	3.7	$0<\mu<9.1$	$0.6<\mu<6.2$
April 5, 1959	9.9	$2.3<\mu<17.5$	$4.4<\mu<11.3$
1959			
October 6, 1959	25.6	$16.0<\mu<35.2$	$14.6<\mu<26.6$
October 20, 1959	26.2	$14.1<\mu<38.2$	$15.6<\mu<33.9$
November 16, 1959	16.3	$0.7<\mu<31.9$	$6.1<\mu<20.6$
February 26, 1960	11.4	$6.9<\mu<15.9$	$7.2<\mu<12.8$
1960			
September 27, 1960	47.2	$32.8<\mu<62.6$	*$64.3<\mu<131.9$
December 1, 1960	27.0	$18.6<\mu<35.4$	*$28.4<\mu<52.7$
March 7, 1961	6.6	$3.8<\mu<9.4$	$4.2<\mu<7.2$

*Value of $\beta<3.0$.

To set confidence limits to estimates of abundance of eggs and larvae with log-transformed data it is first necessary to correct mean log values so that the arithmetic mean will result from the antilog. A correction term is required because the mean of log-transformed data is a geometric rather than an arithmetic mean (Ricker, 1958: ch. 11). Jones (1956) gives the correction term and develops the method used here to calculate confidence limits with log-transformed counts. The equation used to obtain an arithmetic mean ($\bar{n}$) from the log-transformed counts is

$$n=\text{antilog } (\bar{b}+1.1518\ s_b^2)-\beta \qquad (13)$$

---

[1] In this paper the term "log" refers to the logarithm to the base 10.

where $\bar{b}$ is the logarithmic mean value and s_b^2 is the sample variance of the log-transformed counts. It is necessary to subtract β to correct for its addition to counts before making the transformation (equation 11).

Improvement in efficiency of confidence interval estimates of total mortality percentage calculated with log-transformed data can be shown with the October 6, 1959, Harris River sample considered previously. Ninety-percent confidence limits of M_t set with arithmetic counts were

$$6.4\% < M_t < 57.2\%,$$

and the corresponding confidence limits set with log-transformed counts were

$$28.9\% < M_t < 61.0\%.$$

TESTS OF PROPORTIONATE FREQUENCIES

Tests of proportionate frequencies are based on the premise that the proportion of points within a spawning bed occupied by eggs and larvae varies with the total mortality level. If no change in mortality occurs, the following conditions will have been satisfied:

1. There will have been no decrease in the fraction of points populated by eggs or larvae ($Pt1=Pt2=Pt3= \ldots\ldots\ldots$).

2. There will have been no decrease in the fraction of points populated by live eggs or larvae ($At1=At2=At3= \ldots\ldots\ldots$).

3. There will have been no increase in the fraction of points populated by dead eggs or larvae ($Dt1=Dt2=Dt3= \ldots\ldots\ldots$).

Each condition was tested separately with chi square. This was done by classifying each point sampled in accordance with the presence or absence of eggs or larvae. In the examples to be given, points containing three or less eggs and larvae per square foot were counted with zeros; hence, the following three conditions were tested:

1. Presence or absence of three or less total eggs and larvae per square foot.

2. Presence or absence of three or less live eggs and larvae per square foot.

3. Presence or absence of three or less dead eggs and larvae per square foot.

One purpose of the classification scheme was to classify jointly all points containing zero or few specimens. The selection of three or less specimens per square foot for joint classification was arbitrary, however, and the possibility that other criteria for the joint classification of points might improve the tests should not be ignored.

Each of the three conditions was tested by a method described by Bliss and Calhoun (1954: p. 36) and Snedecor (1956: pp. 227–230). Data from the 1959 year class in Harris River are used to illustrate the method in table 7. There was no significant increase in the fraction of points containing three or less total or three or less live eggs and larvae per square foot ($x^2=0.85$ and 1.30). There was a significant decrease, however, in the fraction of points containing three or less dead eggs and larvae per square foot ($x^2=11.16$).

TABLE 7.—*Tests of independence among samples containing three or less eggs and larvae per square foot (Harris River, 1959 year class)*

Date of sampling	Number of points sampled	Three or less total		Three or less live		Three or less dead	
		k_o	p_o	k_o	p_o	k_o	p_o
1959							
October 6	74	44	0.5946	47	0.6351	72	0.9730
October 20	43	25	.5814	26	.6047	38	.8837
November 16	20	13	.6500	14	.7000	18	.9000
1960							
February 26	69	45	.6522	48	.6957	55	.7971

$X^2=\dfrac{\Sigma k_o p_o-\bar{p}_o\Sigma k_o}{\bar{p}_o(1-\bar{p}_o)}$, where p_o=mean of p_o values

X^2 for total = 0.85 (3 degrees of freedom)
X^2 for live = 1.30 (3 degrees of freedom)
X^2 for dead = 11.16 (3 degrees of freedom)

These results suggested that the disappearance of eggs and larvae of the 1959 year class may not have been a major factor in this instance; but the increased fraction of points containing dead eggs and larvae indicated that a significant mortality had occurred nevertheless. The next problem was to determine the periods during which mortality levels had changed. This was done by first setting confidence limits to the number of points containing three or less dead eggs and larvae per square foot (k_o). Where the sample size was adequate, the normal approximation of the binomial distribution was used to set confidence limits. In the present study 90-percent confidence limits of k_o were obtained from the roots of equation (14), i.e.:

$$(\bar{k}_o, \underline{k}_o)=kp_o\pm 1.645\,[kp_o\,(1-p_o)]^{1/2}. \qquad (14)$$

Confidence limits of the fraction of points containing three or less eggs and larvae per square foot (p_0) corresponding to k_0 were obtained by dividing the limits of k_0 by the number of points sampled. Values of k_0 and p_0 for samples of the 1959 year class in Harris River obtained October 6 and 20 and February 26 are given in table 8. Confidence limits were not set to the November 16 sample because of its small size. Inspection of confidence limits of p_0 (table 8) shows that a significant mortality occurred between October 6 and 20 and between October 20 and February 26. Since mortality in these instances was detected with remains of dead eggs and larvae, it was concluded that factors not associated with direct removal of affected specimens from the spawning bed were responsible. If this conclusion is correct then estimates of mortality percentage based on live-dead ratios (M_r) should also indicate that a mortality occurred between October 6 and 20 and between October 20 and February 26. It will be shown shortly that these results are verified by estimates of M_r.

MORTALITY CALCULATED FROM LIVE-DEAD RATIOS

Although estimates of mortality based on ratios of dead eggs and larvae collected in samples (equation 1) are sometimes biased, they do give important evidence of mortality caused by factors not associated with direct removal of affected specimens from spawning beds. Because numbers of eggs and larvae collected from sampling units vary, the necessity of weighting samples for binomial variation before calculating M_r must be considered.

TABLE 8.—*Mean and 90-percent confidence limits of estimated number of points with 3 or less dead eggs and larvae per square foot, Harris River, 1959 year class*

Date of sample	Points sampled	Points containing 3 or less dead specimens per square foot			
		Points (k_0)		Fraction of points (p_0)	
		Mean	90-percent confidence limits	Mean	90-percent confidence limits
1959	*Number*		*Number*		
October 6	74	72	±3.2	0.97	±.04
October 20	43	38	±3.5	.88	±.08
1960					
February 26	69	55	±5.5	.80	±.08

Cochran (1943) has shown that the proper weight applied to each observed fraction of mortality depends on the relative amounts of binomial and extraneous variation in samples. This question was considered for eggs and larvae collected from Harris River and Twelvemile and Indian Creeks (McNeil, 1962), and it was found that equal weight should be given to sampling units from which 10 or more specimens were collected.

Returning to the Harris River 1959 year class example, we find that estimates of M_r support the conclusion that mortality occurred between October 6 and 20 and between October 20 and February 26 (refer to estimates of p_o, table 8). For the three samples considered, estimates of M_r and 90-percent confidence limits of the mean were:

	Percent
Oct. 6, 1959	$M_r = 5 \pm 5$
Oct. 20, 1959	$M_r = 12 \pm 11$
Feb. 26, 1960	$M_r = 27 \pm 11$

DISCUSSION AND CONCLUSIONS

The manner in which total mortality estimated from percentages of dead eggs and larvae collected in samples is biased by disappearance of dead eggs and larvae from the population has been shown algebraically. Estimates of mortality based on live-dead ratios ignore completely mortality that is caused by factors inherently associated with the direct removal of affected eggs and larvae from the population. Decomposition and scavenging also introduce bias to mortality estimates based on the percentage of dead eggs and larvae in samples.

Mortality from all causes occurring over any period of the fresh-water life of pink salmon can be assessed from estimates of abundance. By this method, total fresh-water mortality of pink salmon has been determined in a number of streams by enumerating the adults entering, by estimating their average fecundity, and by enumerating the fry departing. Such data have shown rather conclusively that 75 to 99 percent of total deaths within a population commonly occur in fresh water. An important problem requiring solution is to determine the periods of fresh-water residence during which major changes in the mortality rate occur. Solution of this problem is prerequisite to the identification of the major mortality-causing factors.

With the hydraulic sampler, it is possible to estimate quantitatively the abundance of pink salmon embryos and larvae in spawning beds. Results of unpublished studies conducted by the

Bureau of Commercial Fisheries in Sashin Creek, southeastern Alaska, have shown consistent good agreement between the total fresh-water mortality rate of pink and chum (*O. keta*) salmon estimates by sampling with the hydraulic sampler just prior to emergence of fry and by enumerating fry at a weir.

In Sashin Creek potential egg deposition for the stream as a whole is calculated from the number of adult females enumerated at the weir and their average fecundity. Under some circumstances, however, it may be desirable or necessary to estimate spawning densities within defined segments of the spawning ground. A method of estimating density of females spawning by visual foot survey censuses has been described, but the technique requires further evaluation to determine variability and bias in estimates. The Bureau of Commercial Fisheries is making comparisons between the number of females spawning (estimated by censuses taken on foot surveys) and the number counted at the weir in Sashin Creek. Preliminary unpublished results of these comparisons are not inconsistent with the hypothesis that estimates from foot surveys are essentially unbiased estimates of the true population at spawning densities similar to those observed in Harris River and Indian and Twelvemile Creeks.

Estimates of egg and larval abundance determined from sampling spawning beds are not always as efficient as an investigator might desire. High variability in estimates of abundance and mortality is due primarily to clustering of eggs and larvae in spawning beds. Clustering causes the variance and mean to increase dependently; and confidence limits of estimates of abundance may be widely separated, even with relatively intensive sampling. There is no evidence of reduced tendency of larvae to be clustered, suggesting little if any horizontal scattering of young pink salmon within spawning beds.

Three statistics useful for evaluating mortality in spawning beds have been considered. Total mortality (M_t) is least sensitive as a measure of change in the mortality rate, but it is most useful in determining the magnitude of mortality from all causes. The single binomial parameters of presence or absence of live or dead eggs and larvae at sampling points (p_o) are helpful in two ways. They provide a basis for identifying the periods during which total mortality increased significantly and for determining whether or not such mortality was associated with disappearance of eggs or larvae from the spawning bed. Mortality estimated from live-dead ratios (M_r) is a useful statistic for evaluating mortality caused by factors not associated with the direct removal of dead eggs and larvae from the spawning bed. M_r is biased by the disappearance of dead eggs and larvae from decomposition and scavenging, however. By sampling spawning beds randomly with the hydraulic sampler, the field data can be evaluated by the three independent methods described.

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LITERATURE CITED

Anscombe, F. J.
1949. The statistical analysis of insect counts based on the negative binomial distribution. Biometrics, vol. 5, No. 2, pp. 165–173.

Barnes, H.
1952. The use of transformations in marine biological statistics. Conseil Permanent International pour l'Exploration de la Mer, Journal du Conseil, vol. 18, No. 1, pp. 61–71.

Beall, Geoffrey.
1942. The transformation of data from entomological field experiments so that the analysis of variance becomes applicable. Biometrika, vol. 32, pp. 243–262.
1954. Data on binomial and near binomial distribution. *In* O. Kempthorne, T. A. Bancroft, J. W. Cowen, and J. L. Lush (editors), Statistics and mathematics in biology, pp. 295–302. The Iowa State College Press, Ames.

Beall, Geoffrey, and Richard R. Rescia.
1953. A generalization on Neyman's contagious distributions. Biometrics, vol. 9, No. 3, pp. 354–386.

Bliss, C. I.
1953. Fitting the negative binomial distribution to biological data. Biometrics, vol. 9, No. 2, pp. 176–200.

Bliss, C. I., and D. W. Calhoun.
1954. An outline of biometry. Yale Co-operative Corporation, New Haven, Connecticut, 272 pp. [Processed.]

Briggs, John C.
1953. The behavior and reproduction of salmonid fishes in a small coastal stream. California Department of Fish and Game, Fish Bulletin No. 94, 62 pp.

Cameron, W. M.

1940. The efficiency of fertilization in the natural spawning of Pacific salmon. Fisheries Research Board of Canada, Progress Reports of the Pacific Biological Station and Pacific Fisheries Experimental Station, No. 45, pp. 23–24.

Cochran, William G.

1943. Analysis of variance for percentages based on unequal numbers. American Statistical Association Journal, vol. 38, pp. 287–301.

Davidson, F. A., and S. J. Hutchinson.

1942. Natural reproduction of pink salmon studied at Little Port Walter, Alaska. Ecology, vol. 23, No. 2, pp. 234–235.

Foerster, Russell E., and Andrew L. Pritchard.

1941. Observations on the relation of egg content to total length and weight in the sockeye salmon (*Oncorhynchus nerka*) and the pink salmon (*O. gorbuscha*). Transactions of the Royal Society of Canada, vol. 35, section 5, pp. 51–60.

Hatch, Richard W.

1957. Success of natural spawning of rainbow trout in the Finger Lakes region of New York. New York Fish and Game Journal, vol. 4, No. 1, pp. 69–87.

Hobbs, Derisley F.

1937. Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters. New Zealand—Marine Department, Fisheries Bulletin No. 6, 104 pp.

1940. Natural reproduction of trout in New Zealand and its relation to density of populations. New Zealand—Marine Department, Fisheries Bulletin No. 8, 93 pp.

Hunter, J. G.

1959. Survival and production of pink and chum salmon in a coastal stream. Journal of the Fisheries Research Board of Canada, vol. 16, No. 6, pp. 835–886.

Hutchinson, S. J., and R. F. Shuman.

1942. Reproduction of pink salmon at Little Port Walter, 1941–42. Pacific Fisherman, vol. 40, December 1942, pp. 29–31.

Jones, R.

1956. The analysis of trawl haul statistics with particular reference to the estimation of survival rates. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Réunions, vol. 140, part 1, pp. 30–39.

Martin, John W. (editor)

1959. Stream catalog of eastern section of Ketchikan Management District of Southeastern Ala U.S. Fish and Wildlife Service, Special Scien Report—Fisheries No. 305, 379 pp.

Mathisen, Ole A.

1962. The effect of altered sex ratios on the spaw of red salmon. *In* Ted S. Y. Koo (editor), Stu of Alaska red salmon, pp. 137–246. Universit Washington, Seattle, Publications in Fisheries, 1.

McNeil, William John.

1962. Mortality of pink and chum salmon eggs larvae in Southeast Alaska streams. Ph. Thesis, University of Washington, Seattle, 270

Merrell, T. R., Jr.

1962. Freshwater survival of pink salmon at Sas Creek, Alaska. *In* N. J. Wilimovsky, editor, S posium on pink salmon, pp. 59–72. H. R. M Millan Lectures in Fisheries, University of Brit Columbia, Vancouver.

Neave, Ferris.

1953. Principles affecting the size of pink and ch salmon populations in British Columbia. Jour of the Fisheries Research Board of Canada, v 9, No. 9, pp. 450–491.

1958. Stream ecology and production of anadromo fish. *In* P. A. Larkin (editor), The investigati of fish-power problems, pp. 43–48, Institute Fisheries, University of British Columbia, Va couver, H. R. MacMillan Lectures in Fisheries.

Pritchard, A. L.

1948. Efficiency of natural propagation of the pi salmon, (*Oncorhynchus gorbuscha*) in McClint Creek, Masset Inlet, B.C. Journal of the Fisheri Research Board of Canada, vol. 7, No. 5, p 224–236.

Ricker. W. E.

1954. Stock and recruitment. Journal of the Fis eries Research Board of Canada, vol. 11, No. pp. 559–623.

1958. Handbook of computations for biologic statistics of fish populations. Fisheries Researc Board of Canada, Bulletin No. 119, 300 pp.

Snedecor, George A.

1956. Statistical methods, 5th ed. Iowa State Co lege Press, Ames, 534 pp.

Taft, Bruce, A.

1960. A statistical study of the estimation of abu dance of sardine (*Sardinops caerulea*) eggs. Lin nology and Oceanography, vol. 5, No. 3, p 245–264.

MERISTIC VARIATION IN THE HEXAGRAMMID FISHES

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ABSTRACT

Meristic characters of 300 to 800 specimens of eight hexagrammid fish species are examined for geographic and local variation, and the characters are analyzed for relative variation within and between species. Significant geographic variation occurs frequently and generally is most pronounced in those species with extensive north-south distributions. Sample variation, as measured by the coefficient of variation, is quite consistent for each character both within and between species. Frequency distributions of coefficients enable a general ranking of the characters, with counts of total vertebrae showing the lowest variation and counts of gill rakers the highest. Character variation is comparable with that reported in the literature for other fishes. Geographic variation, where pronounced, appears to be positively correlated with local variation. Character variation probably is affected both by time of embryonic fixation and structural peculiarities of the part.

Students of variation in fishes have usually described, for each population, the fluctuations in range, mode, or mean that are correlated with changes in such environmental factors as geography, temperature, and salinity. A few students have analyzed the correlation between variation of different characters within populations of a species. Both approaches have yielded valuable information. A third approach has been neglected; prior to this study, little attempt has been made to measure the variation of meristic characters within regional samples for the purpose of comparing fish species or populations of fishes. For works of this nature, one must turn to such papers as those on ammonites (Simpson, 1953) and on oreodonts (Baker, 1955).

The term "meristic" has at least two interpretations in the ichthyological literature. A general usage is synonymous with "numerical" or "capable of being counted." A restricted usage applies to those countable characters that appear to be anatomically associated with body somites. Gill raker counts are "meristic" in the general sense, but not in the restrictive. In this paper the more general usage is employed except where otherwise stated.

Data utilized in my analysis became available during taxonomic studies on the nine extant species of the family Hexagrammidae. The family is allied to the Cottidae, and is in the same percoid suborder, Cottoidei. Distributions of the nine species fall within an arc of the North Pacific Ocean above lat. 30° N. (fig. 1). Only eight species are analyzed for geographic variation because insufficient material is available to analyze the ninth species, the Atka mackerel (*Pleurogrammus monopterygius*). The adults of all but one species are demersal and frequent rocky areas to depths of 60 m. or more. The adults of *P. monopterygius* appear largely to have retained the pelagic existence that characterizes hexagrammid larvae.

The three subfamilies that the family may be divided into are the Hexagramminae and the

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Note.—Approved for publication January 6, 1964.

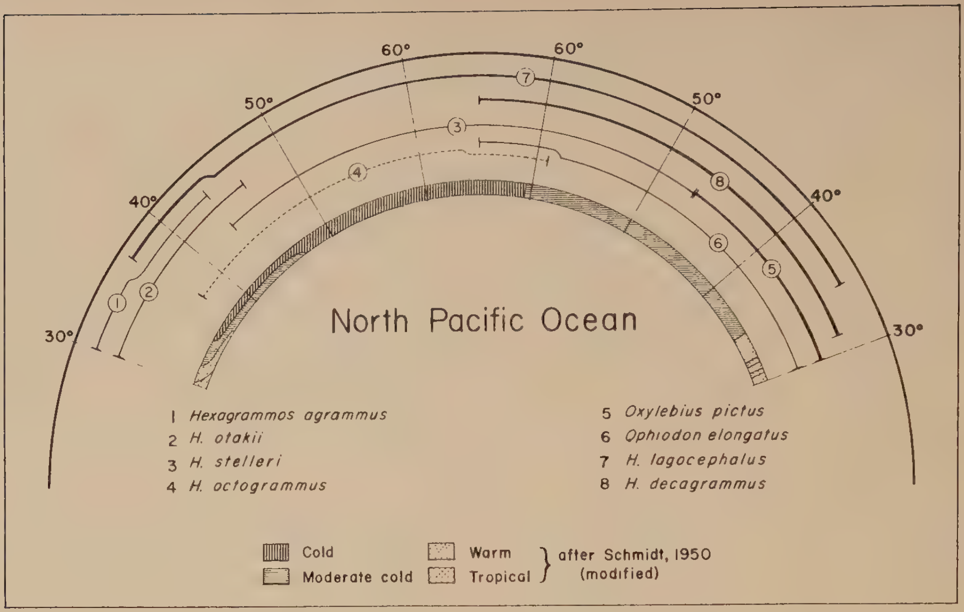

FIGURE 1.—Schematic diagram of geographic ranges in the hexagrammids that are analyzed for geographic variation. Numbers outside the semicircle indicate intersections of lines of latitude with the coastline. Species distributions are indicated by numbered arcs, and the weight of each line is roughly proportional to the degree of geographic variation (as indicated by analyses in figures 2 and 11 and discussed in the text) shown by the species. Limited inshore regions of colder upwelled water are indicated for some lower latitudes of the eastern Pacific Ocean. (Temperature data from Schmidt (1950); slightly modified.)

monotypic Oxylebiinae and Ophiodontinae. The convictfish (*Oxylebius pictus*), sole representative of the Oxylebiinae, is judged to be the most primitive member of the family because of its low meristic counts and the absence of specializations that characterize other representatives of the family. Almost all of the Hexagramminae have multiple lateral lines. In general, the evolutionary trend in the family has been toward the occupation of cold-water niches.

The names of two species depart from conventional usage, in accordance with Quast (1960): *Agrammus agrammus* is called *Hexagrammos agrammus*, and *Hexagrammos superciliosus* is synonymized with its Oriental counterpart, *H. lagocephalus*.

The family Hexagrammidae was judged ideal for meristic analysis because of the limited number of species and the high degree of overlap in their ranges, the ease with which the species could be arranged in phyletic sequence, the meristic diversity of the species, and the relative abundance of specimens in collections.

MATERIAL AND METHODS

The analysis is based on counts of vertebra fin rays, lateral line scales, and gill rakers between 300 and 800 specimens, depending o the character involved. To facilitate compar sons, the geographic ranges are divided arbitrarily, and meristic data from individual localitie are lumped for each division. Nearly all spec mens available were examined. In most instances the collection localities range over th divisions, and in only a few are divisions represented by a single locality. A detailed listin of collection localities appears in the taxonomi section of Quast (1960). Other than gill raker in *Ophiodon elongatus*, discussed below, ther appears to be no association of meristic numbe with sex or size.

The methods of counting are usually thos described by Hubbs and Lagler (1949). Termina dorsal and anal rays are counted as recommende by these authors except for rare specimens tha have the last two elements separated by a spac at their base approximately equal to the spacing of the preceding rays; in these, a count one unit higher is assigned. Pectoral rays and lateral line pored scales are counted on the left side unless that side is damaged. Pores in the skin over the cleithrum and pored scales on the caudal fin posterior to the hypural fan are excluded from the counts of lateral line pored scales. Gill rakers are counted on the first arch of the right side and include rudimentary rakers. (In *Ophiodon elongatus* the anteriormost rakers on the hypobranchial become so indistinct with fish growth that they cannot be counted accurately.) In vertebral counts the urostyle is included as one element, and the first caudal vertebra is identified on X-ray pictures as the anteriormost centrum with a simple haemal spine.

In regard to the analysis of meristic data, frequency distributions approximated the normal in nearly all instances. Cochran's test (Dixon and Massey, 1951) was used for general evaluation of homogeneity of variance for the t and analysis of variance tests. The variances appeared excessively different in an insignificant percentage of the comparisons.

GEOGRAPHIC VARIATION IN THE MEANS OF COUNTS

The means of counts (figs. 2 to 11) [1] vary geographically to some degree in all eight of the hexagrammid species examined. Of 73 species characters analyzed, approximately one-half show geographic variation. The three species with extensive north-south distributions, *Oxylebius pictus*, *Hexagrammos lagocephalus*, and *H. decagrammus*, show the greatest geographic variation both on the criterion of degree of change of counts (discussed in the section on within-sample variation) and on the criterion of the proportion of the counts that vary (fig. 1). Probably *Ophiodon elongatus* also should be included with these species because considerable geographic variation is shown despite only a partial sampling of its range. The other species, which have restricted Oriental distributions or distributions limited to an arc across the North Pacific, show considerably less geographic variation.

In general, the number of meristic elements declines to the south, in agreement with the latitudinal trends commonly reported for fishes in the literature. Numerous deviations from consistent geographic gradients may be noted, however, and the proportions of exceptions vary considerably from species to species.

In *Oxylebius pictus* the highest average for precaudal vertebrae is in the sample from northern and central California, the middle of the geographic range (fig. 2). The average for the northernmost sample is prominently (see footnote 1 for explanation of term) lower than that for the central sample, but the aggregate variation among the samples does not test as significant. The highest average for caudal vertebrae is in the northernmost sample, which is responsible for the high statistical significance of the caudal comparison; and no important differences are apparent between the two southern samples (fig. 3). Similarly, the highest average for total vertebrae occurs in the northernmost sample (fig. 4), where the high average for caudal vertebrae more than compensates for the relatively low average for precaudal vertebrae. No important differences in total vertebrae are demonstrated between the two southern localities. Dorsal fin spines show a definite cline of decreasing counts to the southward (fig. 5). The Puget Sound-Washington sample averages are prominently higher, and the southern-Baja California averages prominently lower than the intermediate samples. A similar trend is shown in the averages of dorsal soft rays (fig. 6), and the trends in spinous and soft rays summate to produce a very definite cline of decreasing total counts to the southward (fig. 7). The northernmost sample of anal fin rays gives the highest count, but the remaining samples show no important differences (fig. 8). Counts of lateral line pored scales shift to lower averages to the south, but the trend is slight and of borderline significance (fig. 9). Counts of pectoral rays show no definite geographic variation in means, but the southern samples appear to have greater ranges (fig. 10). Counts of gill rakers also show no definite geographic variation in means, although the range in

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[1] In figures 2 to 11 the number of specimens in each sample follows the geographic designation. The mean of each sample is bracketed by a black bar that indicates its 95-percent confidence interval (with t correction). The light bar on each side of the mean indicates one standard deviation; the range of counts is given by the heavy lower line. Probabilities shown to the right of each species character are obtained by a t-test where two samples are compared, or by analysis of variance where more than two samples are compared. Coefficients of variation for the samples are indicated in the right-hand column. In the discussion, deviations between paired samples are termed "prominent" when the sample mean with the smaller confidence interval falls outside the 95-percent confidence interval of the mean for the distribution with the larger confidence interval.

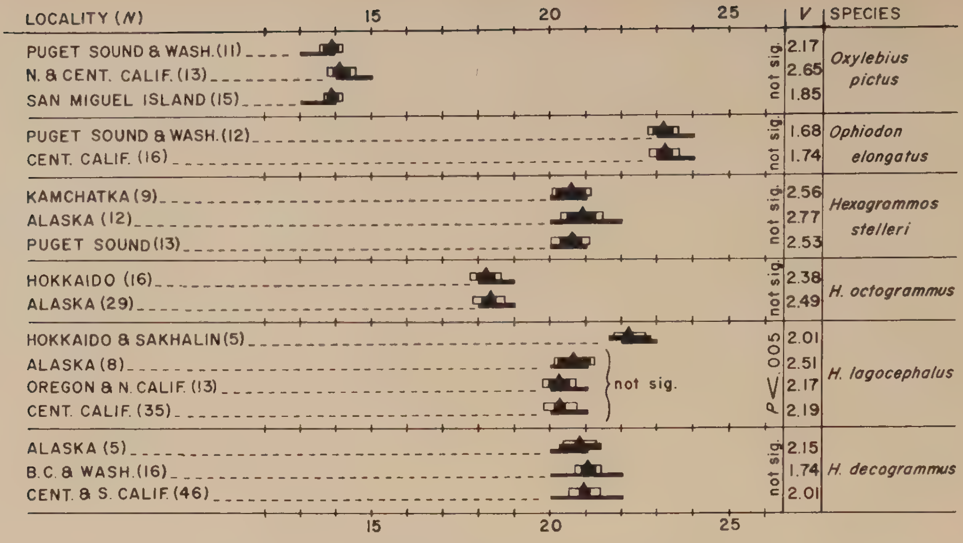

FIGURE 2.—Geographic variation in precaudal vertebrae.

counts is greater in the southern samples (fig. 11).

In *Ophiodon elongatus* no geographic trends are indicated for precaudal, caudal, or total vertebra counts (figs. 2, 3, 4). In contrast, total dorsal ray counts decrease to the southward (fig. 7), apparently because of the decrease in the soft ray portion between the northern and central samples (fig. 6) (where spine counts remain constant) and the decrease in the spinous portion between the central and southern samples (fig. 5) (where soft ray counts remain practically constant). The anal rays follow the pattern of the dorsal fin spines, and a southward decrease in counts is limited to the southern part of the range (fig. 8). No geographi variation is apparent for the averages of latera line pored scales, but the sample from the centra portion of the range is the most variable (fig. 9)— the reverse of the situation for anal rays. Pectora rays show no important variation. Gill rake variation is not assessed because gill raker count change with growth in this species.

Specimens of *Hexagrammos agrammus* were available in limited quantity, and the samples are lumped into two groups. Vertebral comparisons are not made. Counts of spinous dorsal rays are prominently higher in specimens from the

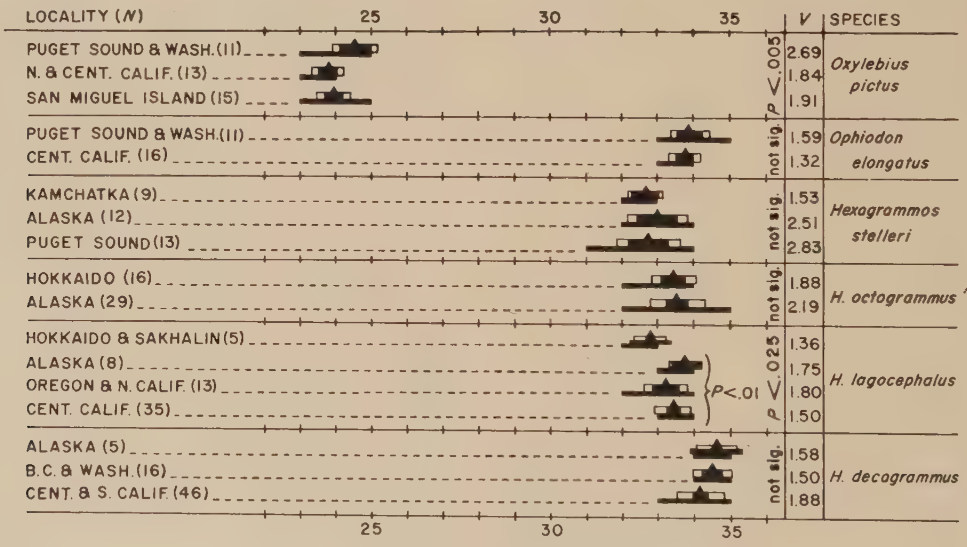

FIGURE 3.—Geographic variation in caudal vertebrae.

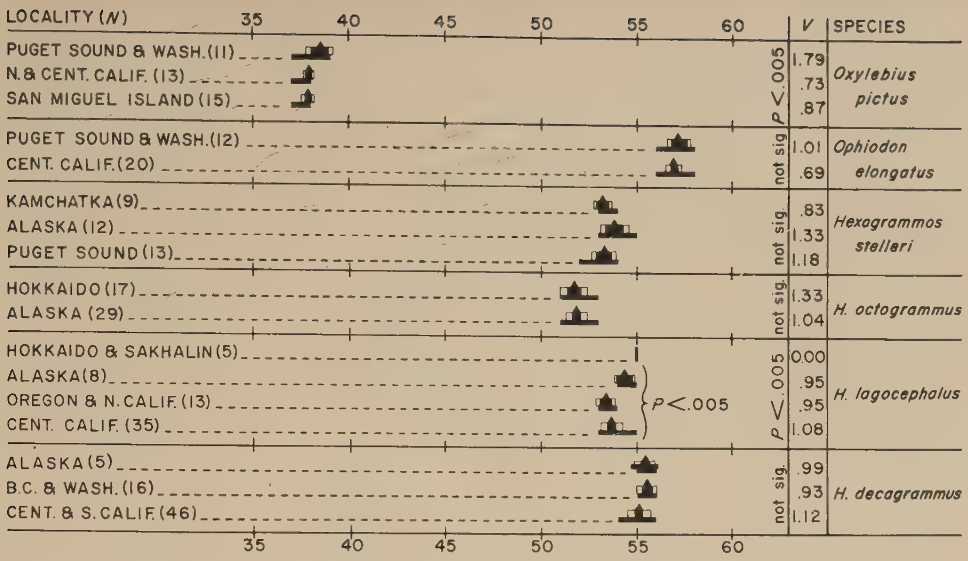

FIGURE 4.—Geographic variation in total vertebrae.

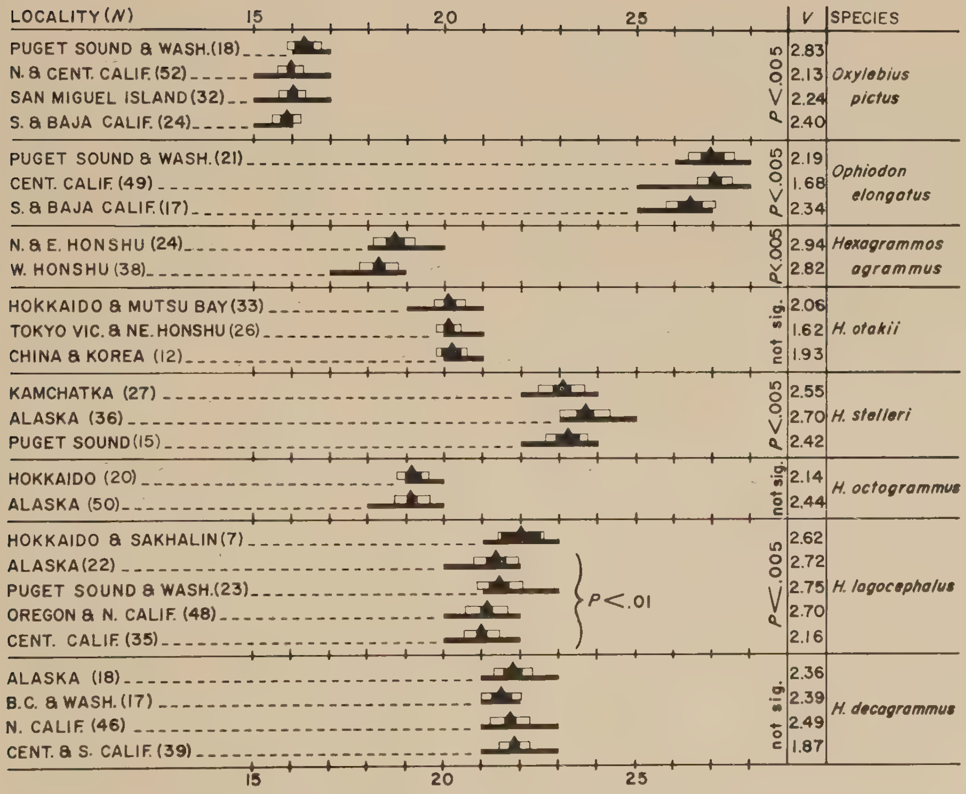

FIGURE 5.—Geographic variation in dorsal fin spinous rays.

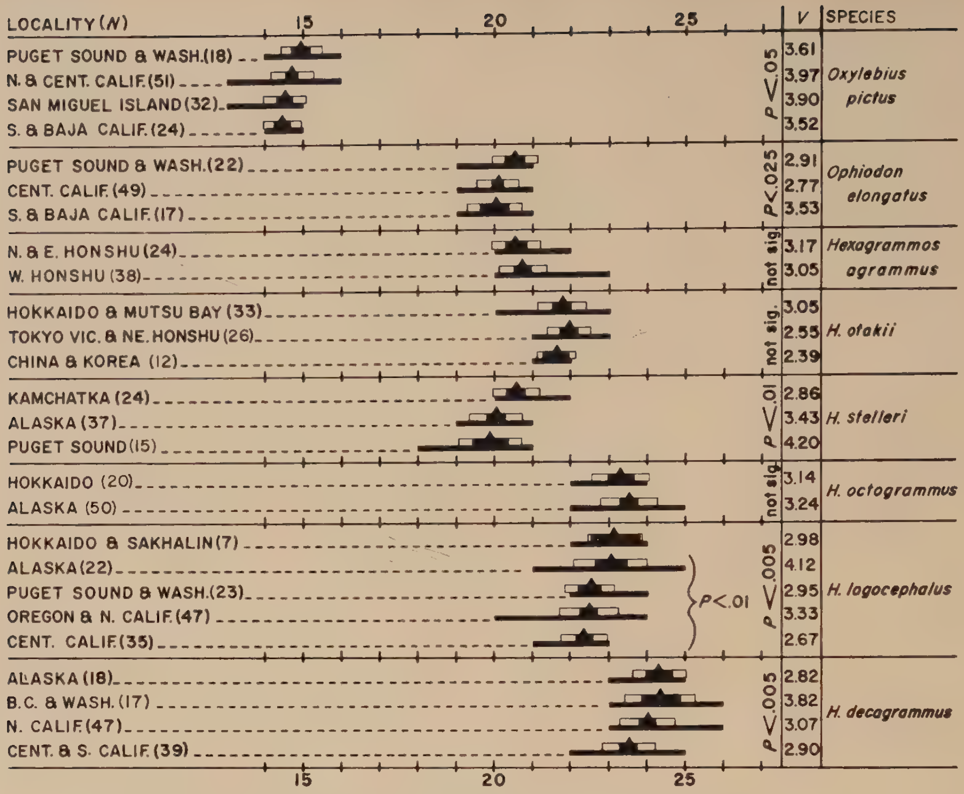

FIGURE 6.—Geographic variation in dorsal fin soft rays.

oceanic side of Honshu (fig. 5), but no differences of corresponding magnitude are apparent for dorsal soft rays or total dorsal rays (figs. 6, 7). Although anal rays are more numerous in the sample from the oceanic side (fig. 8), the difference is not significant. Counts of pectoral rays are prominently lower on the oceanic side of Honshu (fig. 10). No important variation is indicated for lateral line pored scales (fig. 9) or for gill rakers (fig. 11).

Vertebral comparisons are omitted also for *H. otakii*. Counts of dorsal fin rays show no variation worthy of note (figs. 5, 6, 7). Counts of anal rays show significant variation, however, and the mean for counts from the eastern coast of Honshu is prominently higher than the mean for Hokkaido or the mainland (fig. 8). (Although similar in mean value, the counts from the mainland and Hokkaido differ markedly in coefficient of variation.) Lateral line pored scales show a definite shift toward lower counts in the regions from Hokkaido through Honshu to China and southern Korea (fig. 9). Counts of pectoral rays show no significant differences (fig. 10). Counts of gill rakers are prominently higher in the Hokkaido-Mutsu Bay sample than in the northeastern Honshu sample (fig. 11).

The three geographic samples of *H. stelleri* differ relatively little in latitude. No significant overall differences are indicated for counts of precaudal, caudal, or total vertebrae (figs. 2, 3, 4), although the total counts for Alaska average prominently higher than those for Kamchatka and Puget Sound. Averages for counts of total dorsal fin rays from Kamchatka and Alaska (fig. 7) are similar, although there are prominently opposing trends in spines and soft rays between the two localities (figs. 5, 6). The Puget Sound sample has prominently lower total dorsal ray counts than either Kamchatka or Alaska. No important differences are evident in the averages for anal fin rays or lateral line pored scales (figs. 8, 9). In pectoral rays, the Alaska sample has the prominently highest average (fig. 10). Gill raker counts are prominently lower in the Alaska sample than in the one from Kamchatka, but the three samples of this character do not differ significantly in the aggregate (fig. 11).

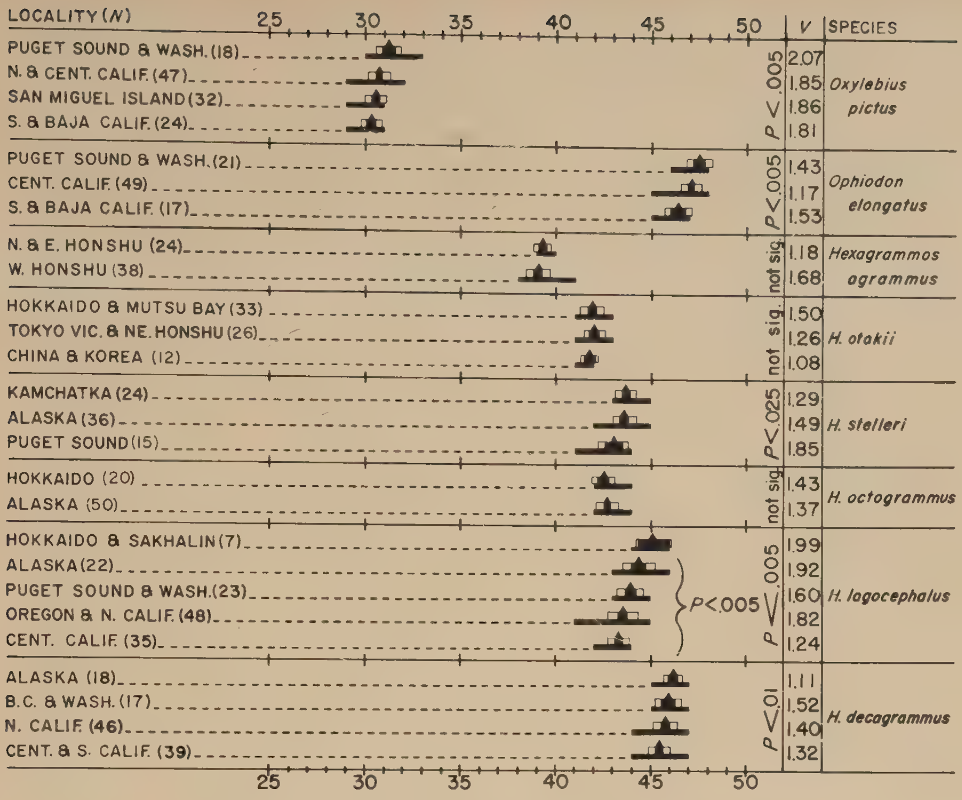

FIGURE 7.—Geographic variation in total dorsal rays.

Samples of *H. octogrammus* from the Orient and Alaska show few important meristic differences. Average counts for vertebrae (figs. 2, 3, 4), dorsal fin rays (figs. 5, 6, 7), lateral line pored scales (fig. 9), and gill rakers (fig. 11) are quite similar in the two samples. Only counts of anal and pectoral rays show differences of possible significance, and the Oriental sample gives the highest average n each instance (figs. 8, 10).

In *H. lagocephalus*, a sharp discontinuity is shown between samples of counts of precaudal vertebrae from Hokkaido-Sakhalin and Alaska (fig. 2). The dramatic difference may warrant subspecific recognition of the eastern and western Pacific representatives. Adequate data are not available from intermediate points, however, and a cline actually may exist between the two regions. In contrast, no important differences are apparent between samples of precaudal counts from the northeastern Pacific. A reciprocal relationship between precaudal and caudal counts, similar to hat noted for *Oxylebius pictus*, is apparent in the Oriental and eastern Pacific samples (figs. 2, 3). Prominent differences exist between all samples of total vertebral counts, with the Oriental counts the highest and the Alaskan specimens second highest (fig. 4). Definite clines of decreasing counts from Hokkaido to central California are apparent in dorsal fin rays (figs. 5, 6, 7), and the clines remain significant whether the Oriental samples are included or not. Anal fin rays show a similar cline except for a slight increase in means between the Oregon-northern California sample and the central California sample (fig. 8); the variation in anal fin rays is also significant whether the Oriental sample is considered or not. Averages for lateral line pored scales show a variation pattern similar to that of anal fin rays, with the highest average in the Orient (fig. 9). Pectoral rays also have the highest average in the Oriental sample, and the Oriental counts are nearly disjunct from the distributions obtained from the eastern Pacific, where no variation is apparent (fig. 10). Little variation is visible in the numbers of gill rakers (fig. 11).

In *H. decagrammus* vertebral counts show a low degree of geographic variation, but caudal and total vertebral counts are prominently lower from

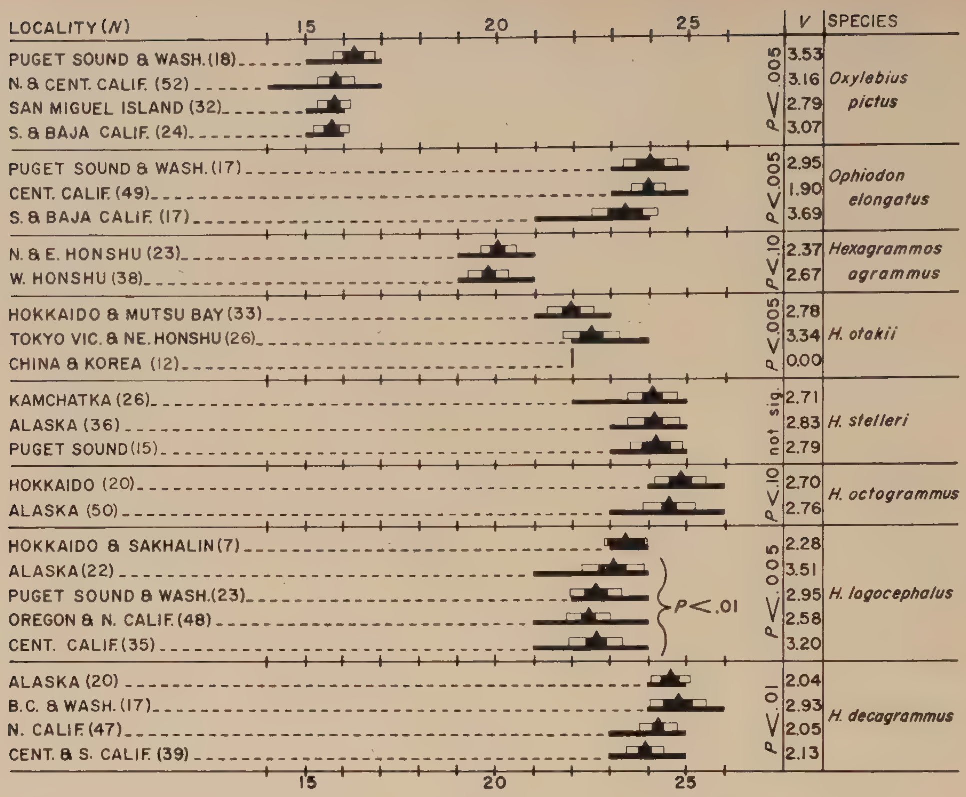

FIGURE 8.—Geographic variation in anal fin rays.

California than from British Columbia and Washington (figs. 2, 3, 4). Numbers of dorsal fin spinous rays show no differences worthy of emphasis, but the dorsal soft rays show a prominent decrease in number in the southern part of the species geographic range (figs. 5, 6). Total dorsal fin ray counts show a cline of numerical decrease to the south (fig. 7); the shift apparently is caused by a slight decline in spinous ray counts in the northern part of the geographic range (where soft ray counts remain constant) and a prominent decrease in soft ray counts in the southern part (where the shift in spinous counts opposes but does not completely compensate for the shift in the number of soft rays). Anal fin rays follow the dorsal soft ray pattern and show a decrease in counts only in the southern half of the geographic range (fig. 8). A general north-south cline of decreasing numbers of lateral line pored scales is evident, although the differences between adjacent samples are slight (fig. 9). Similar clines are noticeable in numbers of pectoral rays and gill rakers, but the aggregate variation in gill rakers does not test as significant (figs. 10, 11).

The foregoing examination of meristic variation in the hexagrammids demonstrates that the manifestation of this variation is quite complex and that shifts in means and ranges of counts between geographic samples are not always predictable. The tendency for meristic counts to be greater in the more northern and more western Pacific localities is obvious. Sampling error may be responsible for some of the contradictory trends noted between neighboring samples and, in part, for the poor correspondence in details of variation found between the species over shared portions of their geographic ranges. Numerous instances of poor correspondence between trends in counts of total elements and the numbers of elements in their sections also are noted. For example, a southward decrease in total vertebrae in *Oxylebius pictus* over the two northernmost localities (fig. 4) reflects a considerable decrease in the average number of caudal vertebrae (fig. 3), and the average number of precaudal vertebrae may actually vary in the opposite direction over the same region (fig. 2). As a corollary, the apparent lack of geographic variation in a total count may mask

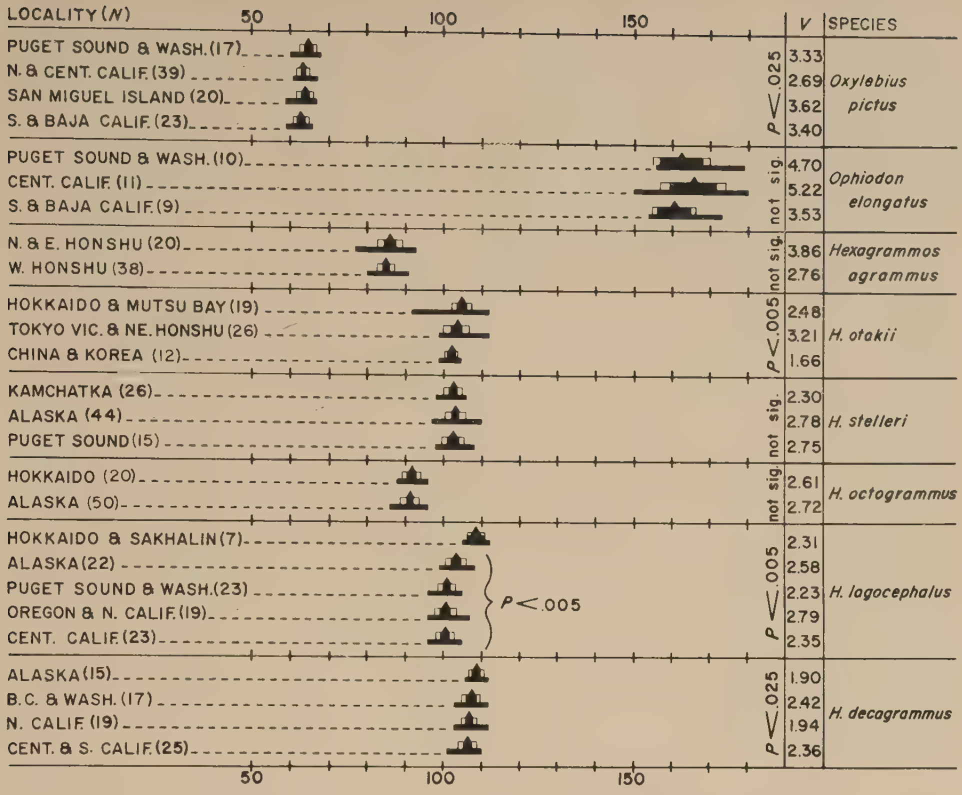

FIGURE 9.—Geographic variation in lateral line pored scales.

significant opposing geographic trends in its sections such as, for example, the pattern of dorsal fin variation in *H. stelleri* between Kamchatka and Alaska (figs. 5, 6, 7). Significant geographic variation is most frequent in the dorsal fin, second most frequent in the anal fin, and least frequent in the gill rakers.

WITHIN-SAMPLE VARIATION OF MERISTIC CHARACTERS

In addition to the mean, a measure of dispersion is necessary to characterize fully a normal frequency distribution, and the study of variation in organisms is not complete without some such estimate of the variation of characters about their sample averages. This estimate provides an index to the stability of the processes that lead to the mean values of anatomical features used to characterize populations or species. Statistics on meristic characters in fishes have the advantage that these characters are easily counted and their frequency distributions commonly approximate normal.

Simpson (1953) raised an important question concerning the role of variation in evolution without arriving at any definite conclusions. He asked whether a highly variable population would offer more materials for evolution of new species than one that is less variable. This and other questions regarding variation in phyletic lines of animals are responsible for the following analysis. In order to examine the hexagrammid fishes in this respect, coefficients of variation are calculated for meristic characters from the available geographic samples of the species. This coefficient gives the standard deviation of a sample as a percentage of the mean. For a discussion of its use, see Simpson, Roe, and LeWontin (1960).

Interspecific and Intraspecific Similarities in Variation Coefficients of a Character

A comparison of the character coefficients of variation for all hexagrammid samples (see figs. 2 to 11 and table 1) demonstrates that for each character (e.g. total vertebral count) there is a remarkable consistency in the degree of variation shown (1) between geographic samples of a species and (2) between the species themselves. Also,

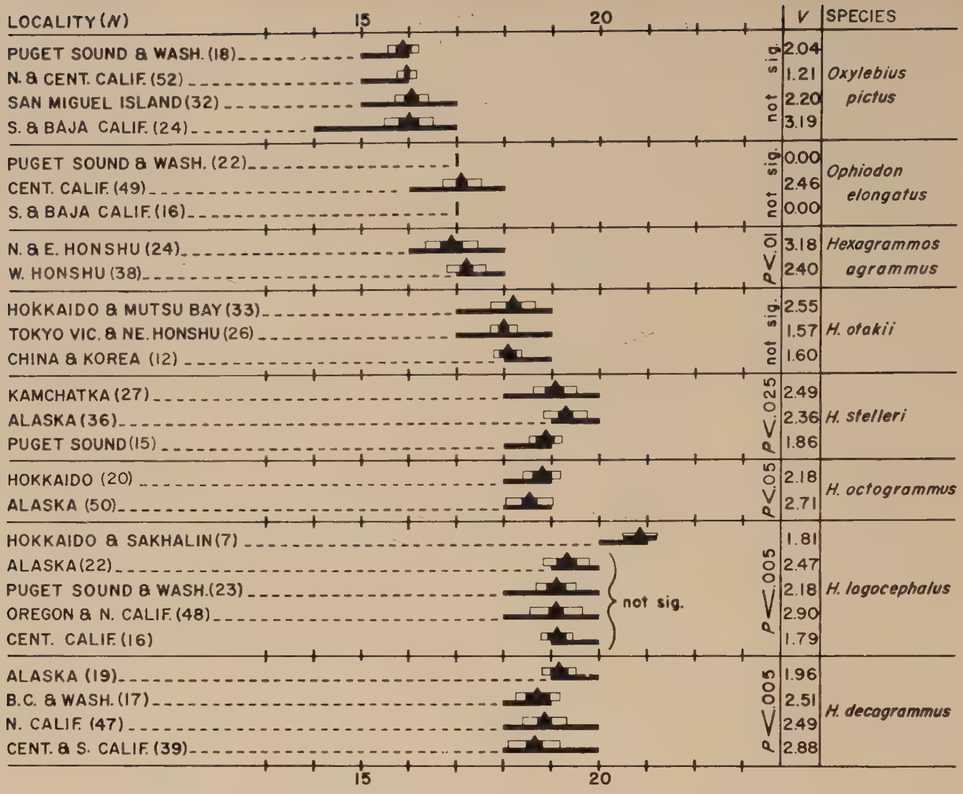

FIGURE 10.—Geographic variation in pectoral rays.

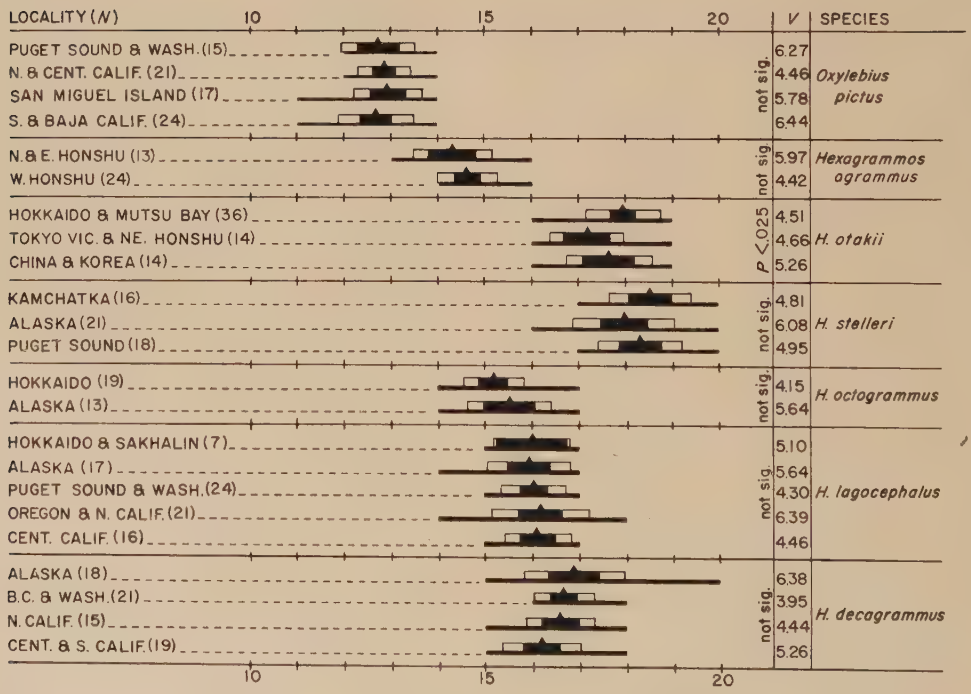

FIGURE 11.—Geographic variation in gill rakers.

each of the characters (e.g. number of anal fin rays, number of caudal vertebrae) appears to have a characteristic modal value for variation that usually differs in some degree from that for each of the other characters. Because of the consistency in variation between similar counts and the difference in variation between different counts, the samples form a hierarchial pattern when plotted on a frequency diagram (fig. 12). Similar results are obtained by ranking for each species, in order of numerical value, the averages of each set of character coefficients. In nearly all rankings, vertebral values are lowest, and total dorsal rays adjoin; whereas gill raker values are consistently highest.

The study shows an interesting relationship between the variation of entire counts, namely total dorsal spines and total vertebrae, and that of their serial components. In each comparison of this type (fig. 12), the range of coefficients for the whole count is distinctly lower than for either of its sections. The greater variation shown by components of the whole counts may be explained in part by an apparent variability in the developmental fate of the transitional elements; that is, whether a given element will develop into the type characteristic of the anterior or the posterior section. This instability, mentioned above as introducing some exceptions to the general geographic trends of the means, is presumably not linked to body metamerism, but rather to the processes that influence the fate of the boundary elements. Although according each section of entire counts high values for variation, the instability of transitional elements has no effect on the variability of entire counts because the total number of elements is not affected. As an example, the frequency with which a boundary element becomes either a dorsal spine or a dorsal soft ray, or a precaudal or a caudal vertebra, has no effect on the total number of elements in the dorsal fin or in the vertebral column. Gosline (1947) described a negative correlation between the number of anterior and posterior elements for *Etheostoma exile*, and Hubbs and Hubbs (1954) described it for the kelp perch, *Brachyistius frenatus*.

Table 1.—*Variation data on hexagrammid species not presented in figures 2 to 11* [1]

Species and character	Number	Mean and range of counts	Coefficient of variation
Hexagrammos agrammus:			
Precaudal vertebrae	32	18.81 (18–20)	2.84
Caudal vertebrae	32	29.22 (28–30)	2.26
Total vertebrae	32	48.03 (46–50)	1.45
Hexagrammos otakii:			
Precaudal vertebrae	32	20.08 (20–21)	1.44
Caudal vertebrae	12	31.58 (31–32)	1.63
Total vertebrae	12	51.67 (51–52)	0.95
Pleurogrammus monopterygius:			
Dorsal spines	34	22.18 (24–29)	3.42
Dorsal soft rays	33	26.61 (24–29)	3.75
Total dorsal rays	33	48.79 (47–50)	1.43
Total anal rays	31	26.10 (25–27)	2.68
Pectoral rays	34	25.09 (24–26)	2.67
Precaudal vertebrae	8	26.62 (26–27)	1.95
Caudal vertebrae	8	33.62 (33–35)	2.21
Total vertebrae	8	60.25 (60–61)	0.77
Lateral line pored scales	38	152.08 (139–166)	4.13
Gill rakers	31	24.90 (22–27)	4.79

[1] Data are from collections from single geographic locations only: *Hexagrammos agrammus*, Kyogo Misaki, Japan; *H. otakii*, "Tokyo," Japan; *Pleurogrammus monopterygius*, Alaska.

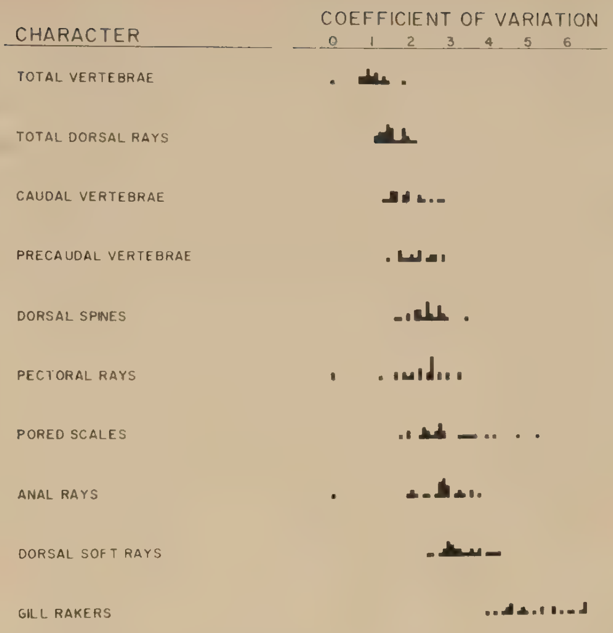

Figure 12.—Frequency diagram of variation coefficients for samples of hexagrammid meristic counts. Characters arranged in order of increasing variability.

The values for the variation of meristic characters of the same body region are not necessarily similar. Although the caudal vertebrae and the anal and soft dorsal fins are of similar extent and occupy the same body region in hexagrammid fishes, an overall comparison of the frequency distributions of the character variation coefficients (fig. 12) demonstrates that variation in the numbers of caudal vertebrae throughout the family generally is less than in anal rays and dorsal soft rays.

Meristic Variation of Hexagrammids Compared With That of Other Fishes

In general, meristic variability in characters of the hexagrammid fishes agrees with or is lower than that for the same characters in fishes of several other families and orders randomly selected from the literature (table 2). Coefficients of variation (*V*) for vertebral counts are relatively uniform and low among all samples of the various families, with two exceptions: In *Fundulus*, especially in laboratory-reared samples, and in some samples of the flatfish *Parophrys vetulus*, the coefficients are unusually high. Variation in the number of dorsal spines, as compared with the hexagrammids, is lower in five families and higher in two. The range of coefficients for numbers of dorsal fin soft rays in hexagrammids approximates that of herring, flatfishes, some scorpaenids, one cottid, and one goby, but is considerably lower than that of one serranid, two percids, and two scorpaenids. Variation in numbers of anal rays, lateral line pored scales, pectoral rays, and gill rakers in hexagrammids generally is below that of the other examples.

Overall Variation in the Hexagrammids and Its Relationship to Evolution Within the Family

A crude estimate of general meristic variability was attempted for each of the nine species of Hexagrammidae by calculating character by character the number of positive and negative deviations of all samples of each species from the family averages for variation. It was assumed that any species having overall high or low values for variation also will have unusually high or low totals of values above or below the family means. When the frequencies of positive and negative deviations were tested with the chi-square distribution, a significant departure from the distribution of values expected in a homogeneous sample was found at the 95-percent level, indicating that some species probably have greater allotments of variation coefficients above or below the family means than would be expected by chance alone. The data indicate that the values for *Oxylebius pictus* and *Hexagrammos decagrammus* are in large part responsible for the high chi-square value. The two species depart strongly from the family averages for meristic variation, but in different directions: In *O. pictus*, 12 out of 15 coefficients are above the family means; in *H. decagrammus*, 13 out of 15 coefficients are below.

Because the average counts for meristic characters in the two species are markedly dissimilar, another interpretation of the differences in variation between the two species, as indicated by *V*, would be necessary if the standard deviations of character samples of *O. pictus* and *H. decagrammus* were the same. In this instance, the divisor of the variation equation would be larger for characters of *H. decagrammus* because of the higher counts in this species, and hence would accord this species lower values for variation. The data disclose, however, that the standard deviations for characters of *O. pictus* are not the same as for those of *H. decagrammus*, and that the latter are consistently higher (table 3). The lower values for *V* in *H. decagrammus* are the result of the disproportionate differences in means and standard deviations of the two species: the increase in standard deviations of character samples between *O. pictus* and *H. decagrammus* does not quite keep pace with that of the mean values of their meristic characters.

The differences in variation between *O. pictus* and *H. decagrammus* suggest that the more highly evolved form may be less variable. *Oxylebius pictus* is interpreted as being the most primitive living species in the family because of its low meristic counts and single lateral line. In contrast, *H. decagrammus* has these characters in an apparently more derived condition. However, since it is not known to what extent the differences in variability between the two species are due to environmental rather than to genetic causes, the significance of the differences is questionable. In addition, other hexagrammid species that contrast nearly as strongly in subjective estimates regarding their evolutionary status show no corresponding general differences in their variation. It must be concluded that any relationships between variation and evolution in the Hexagrammidae are too subtle or too complex to be reliably indicated by such gross numerical analyses.

Relationship Between Variation Within Samples and Geographic Variation of a Character

Considerable taxonomic significance may pertain to the possible relationships between the variation within regional or local samples of a character, as measured by the coefficient of variation, and the variation between samples taken over the entire geographic range of a species. A

TABLE 2.—*Comparison of coefficients of variation (V) for hexagrammids with those for other fishes, as calculated from data randomly selected from the literature*

Character, family, and species	Samples (specimens)	Sample averages	Range of *V*
Vertebral elements:			
Hexagrammidae	20 (327)	38–60	0.7–1.8
Clupeidae:			
Clupea pallasi (Hubbs, 1925)	5 (847)	52–53	1.2–1.5
Sardinops caerulea (Hubbs, 1925)	2 (494)	52	1.1–1.2
Engraulidae:			
Engraulis mordax (Hubbs, 1925)	2 (729)	46	1.3–1.5
Cyprinodontidae:			
Fundulus heteroclitus (Gabriel, 1944):			
Laboratory-reared specimens	3 (932)	32–33	2.3–2.9
Wild population	1 (105)	32	2.0
Bothidae:			
Citharichthys stigmaeus (Taylor, 1957)	25 (1,988)	37–38	.9–1.8
Pleuronectidae:			
Eopsetta jordani (Taylor, 1957)	15 (1,486)	43	.8–1.9
Microstomus pacificus (Taylor, 1957)	5 (266)	52	1.2–1.7
Parophrys vetulus (Taylor, 1957)	27 (2,130)	42–44	1.1–2.8
Percidae:			
Fourteen species (Bailey and Gosline, 1955)	14 (405)	36–43	.7–1.5
Etheostoma exile (Bailey and Gosline, 1955)	1 (1,000)	37	1.9
Cottidae:			
Leptocottus armatus (Hubbs and Hubbs)[1]	12 (1,938)	36–38	1.1–1.8
Dorsal spines:			
Hexagrammidae	27 (799)	16–27	1.6–3.4
Serranidae:			
Roccus saxatilis (Raney, 1957)	12 (1,320)	9	3.0–6.0
Percidae:			
Etheostoma exile (Gosline, 1947)	1 (1,000)	10	7.9
Percina nigrofasciata (Crawford, 1956)	19 (1,720)	12	4.1–5.9
Scorpaenidae:			
Ocosia, 2 spp. (Matsubara, 1943)	2 (75)	15–16	3.4
Setarches, 2 spp. (Matsubara, 1943)	2 (283)	12	.7–1.4
Cottidae:			
Leptocottus armatus (Hubbs and Hubbs[1])	12 (1,754)	7–8	4.6–8.6
Gobiidae:			
Clevelandia ios (Prasad, 1958)	4 (188)	4–5	.9–1.2
Dorsal soft rays:			
Hexagrammidae	27 (795)	14–27	2.4–4.2
Clupeidae:			
Clupea pallasi (Hubbs, 1925)	2 (390)	18	3.7–4.1
Serranidae:			
Roccus saxatilis (Raney, 1957)	4 (294)	11	4.3–5.0
Percidae:			
Etheostoma exile (Gosline, 1947)	1 (1,000)	11	6.0
Percina nigrofasciata (Crawford, 1956)	19 (1,698)	11–12	4.2–6.1
Bothidae:			
Citharichthys stigmaeus (Taylor, 1957)	25 (2,268)	82–88	2.5–5.8
Pleuronectidae:			
Eopsetta jordani (Taylor, 1957)	16 (1,337)	90–93	2.2–3.4
Microstomus pacificus (Taylor, 1957)	5 (255)	103–105	3.2–4.6
Parophrys vetulus (Taylor, 1957)	27 (2,083)	77–83	3.2–5.6
Scorpaenidae:			
Ocosia, 2 spp. (Matsubara, 1943)	2 (75)	8–9	5.6–7.7
Setarches, 2 spp. (Matsubara, 1943)	2 (283)	10	.7–3.4
Cottidae:			
Leptocottus armatus (Hubbs and Hubbs[1])	12 (1,753)	16–18	3.0–4.0
Gobiidae:			
Clevelandia ios (Prasad, 1958)	4 (188)	16–17	3.0–3.6
Anal rays, total or soft rays only:			
Hexagrammidae	27 (816)	16–26	1.9–3.7
Clupeidae:			
Clupea pallasi (Hubbs, 1925)	2 (390)	16–17	5.0–5.4
Cyprinodontidae:			
Fundulus, 2 spp. (Brown, 1958)	15 (368)	10	2.6–6.1
Serranidae:			
Roccus saxatilis (Raney, 1957)	4 (294)	10–11	3.8–5.0
Percidae:			
Etheostoma exile (Gosline, 1947)	1 (1,000)	8	8.6
Bothidae:			
Citharichthys stigmaeus (Taylor, 1957)	25 (2,265)	63–70	2.1–4.1
Pleuronectidae:			
Eopsetta jordani (Taylor, 1957)	15 (1,331)	70–73	2.6–5.4
Microstomus pacificus (Taylor, 1957)	5 (258)	85–87	3.3–4.5
Parophrys vetulus (Taylor, 1957)	27 (2,058)	57–62	3.1–6.0
Scorpaenidae:			
Ocosia, 2 spp. (Matsubara, 1943)	2 (75)	6	5.7–6.4
Setarches, 2 spp. (Matsubara, 1943)	2 (283)	5	2.3–2.4
Cottidae:			
Leptocottus armatus (Hubbs and Hubbs[1])	12 (1,752)	15–18	3.1–4.1
Gobiidae:			
Clevelandia ios (Prasad, 1958)	4 (188)	16	3.5–3.8
Bleniidae:			
Istiblennius edentulus (Strasburg, 1955)	3 (280)	22	2.2–2.8
Acanthuridae:			
Three species (Randall, 1955, 1956)	6 (249)	20–26	2.0–3.0
Lateral line scales or pored scales:			
Hexagrammidae	27 (620)	63–165	1.7–5.2
Cyprinidae:			
Notropis spilopterus (Gibbs, 1957a)	16 (1,157)	36–39	1.7–2.7
Notropis venustus (Gibbs, 1957b)	19 (1,149)	36–42	1.7–4.3
Percidae:			
Etheostoma exile (Gosline, 1947)	1 (1,000)	53	5.1
Percina nigrofasciata (Crawford, 1956)	19 (1,745)	52–63	4.1–6.1
Scorpaenidae:			
Ocosia, 2 spp. (Matsubara, 1943)	2 (75)	15	6.9–11.6
Setarches, 2 spp. (Matsubara, 1943)	2 (278)	25–26	5.2–5.4
Pectoral rays:			
Hexagrammidae	27 (803)	16–25	1.2–3.2
Cyprinidae:			
Notropis spilopterus (Gibbs, 1957a)	22 (2,757)	14	3.0–6.1
Notropis venustus (Gibbs, 1957b)	23 (2,575)	14–16	3.1–8.8
Percidae:			
Percina nigrofasciata (Crawford, 1956)	19 (1,702)	28–29	2.5–4.5
Bothidae:			
Citharichthys stigmaeus (Taylor, 1957)	25 (2,330)	11–12	4.6–7.2
Pleuronectidae:			
Eopsetta jordani (Taylor, 1957)	16 (1,441)	12–13	2.3–7.9
Microstomus pacificus (Taylor, 1957)	5 (272)	10	5.8–7.9
Parophrys vetulus (Taylor, 1957)	21 (1,704)	12	4.3–7.1
Scorpaenidae:			
Ocosia, 2 spp. (Matsubara, 1943)	2 (75)	12	2.6–3.7
Setarches, 2 spp. (Matsubara, 1943)	2 (278)	22	2.7
Cottidae:			
Leptocottus armatus (Hubbs and Hubbs[1])	12 (4,256)	18–19	2.5–3.2
Gobiidae:			
Clevelandia ios (Prasad, 1958)	4 (188)	19	3.6–4.9
Gill rakers:			
Hexagrammidae	24 (511)	13–25	3.9–6.4
Scorpaenidae:			
Ocosia, 2 spp. (Matsubara, 1943)	2 (65)	8–10	10.8–13.1
Setarches, 2 spp. (Matsubara, 1943)	2 (283)	13	5.5–6.9

character that varies little within regional or local samples assumes greater significance when associated with extensive geographic variation. An index of variation within samples of species characters is available in the form of averaged coefficients of variation of the samples. An index of geographic variation may be obtained by dividing the maximum difference between sample means of a species character by the midrange of the character means. The value obtained, like the coefficient of variation, expresses the difference as a percentage of the mean or central value. To determine what relationships may exist between these two types of variation, averaged values of the coefficient of variation were compared with the index of geographic variation for each of nine strictly meristic counts in the four species that display marked geographic variation—*Oxylebius*

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[1] Hubbs, Carl L., and L. C. Hubbs. Analysis of meristic variation in *Leptocottus armatus*, a fish of western North America. Manuscript being prepared for publication, Scripps Institution of Oceanography, La Jolla, Calif.

TABLE 3.—*A comparison of mean values for the standard deviation in samples of* Oxylebius pictus *and* Hexagrammos decagrammus

Character	*O. pictus*			*H. decagrammus*			Proportionate increase	
	Standard deviation		Mid-range of count	Standard deviation		Mid-range of count	Standard deviation	Mid-range of count
	Number	Mean		Number	Mean			
Dorsal spines	4	0.387	16.0	4	0.487	22.0	1.26	1.37
Dorsal soft rays	4	.550	14.5	4	.760	24.0	1.38	1.65
Total dorsal rays	4	.585	31.0	4	.612	45.5	1.05	1.47
Anal rays	4	.498	15.5	4	.560	24.5	1.12	1.58
Pectoral rays	4	.341	15.5	4	.462	19.0	1.35	1.22
Precaudal vertebrae	3	.310	14.0	3	.407	21.0	1.31	1.50
Caudal vertebrae	3	.520	24.0	3	.470	34.0	1.09	1.42
Total vertebrae	3	.430	38.0	3	.564	55.0	1.31	1.45
Lateral line pored scales	4	2.080	63.5	4	2.310	107.5	1.11	1.69
Gill rakers	4	.735	12.5	4	.832	17.5	1.13	1.40
Average increase							1.21	1.47

pictus, *Ophiodon elongatus*, *Hexagrammos lagocephalus*, and *H. decagrammus* (table 4). The comparison by means of the rank-correlation test (Dixon and Massey, 1951) indicates a probable positive correlation between the two types of variation for *H. decagrammus* and *Ophiodon elongatus*, and *H. lagocephalus* if the Oriental sample is excluded. A positive correlation may also exist in *Oxylebius pictus*. The pooled data for all four species show a high level of significance. It seems, therefore, that the two types of variation are positively associated in the hexagrammid fishes and that characters exhibiting the greatest shift in means geographically, by the above criteria, also tend to have the highest average values for the coefficient of variation in the regional samples. This conclusion suggests that the other species of hexagrammids, whose characters exhibit comparable variation on a local basis, have a potential for geographic variation that is unrealized.

The eight species contrast markedly in the total amount of geographic variation they demonstrate relative to their local variation. A comparison is possible if the index of geographic variation of each species character is divided by the corresponding index of local variation and all the quotients are averaged for each species (table 5). The four species with extensive north-south distribution, *Oxylebius pictus*, *Ophiodon elongatus*, *Hexagrammos lagocephalus*, and *H. decagrammus*, generally show the highest values for character variation geographically. This finding is schematized in figure 1. The ranking of species is similar whether the sectional counts are used or not. The variation data for *H. lagocephalus* emphasize, once again, the meristic differences between representatives from the eastern Pacific (formerly *H. superciliosus*) and those from the Orient (table 5). East-west variation accounts for much of the very high values attributed to *H. lagocephalus*, and the values correspond much more closely to those of the other species when the Oriental sample is excluded.

TABLE 4.—*Rank correlation between local and geographi variation in meristic characters in four species of Hexagrammidae*

[Meristic characters are ranked for both types of variation (see text) within the four species and also over the four species (overall ranking in parentheses). Highest values represent lowest ranks. Significance levels o within-species data: 5-percent=0.600; 1-percent=0.783. Significance levels of overall data: 5-percent=<0.306; 1-percent=<0.432. (From Dixon and Massey, 1951)]

Character	*Oxylebius pictus*		*Ophiodon elongatus*		*Hexagrammos lagocephalus*		*Hexagrammos decagrammus*	
	Local	Geographic	Local	Geographic	Local	Geographic	Local	Geographic
Precaudal vertebrae	5(17)	7(25)	5(26)	9(36)	6(18)	1(1)	6(23)	8(31)
Caudal vertebrae	7(20)	3(12)	6(29)	7(34)	8(28)	9(17)	7(27)	7(29)
Total vertebrae	9(32)	8(28)	8(34)	8(35)	9(36)	8(16)	9(33)	9(32)
Dorsal spines	4(13)	6(18)	4(22)	5(23)	3(10)	4(4)	4(15)	6(27)
Dorsal soft rays	1(2)	2(11)	2(7)	3(21)	1(4)	7(10)	1(5)	2(9)
Total dorsal rays	8(24)	5(15)	7(30)	4(22)	7(25)	6(6)	8(31)	5(26)
Anal rays	3(6)	1(7)	3(9)	2(20)	2(8)	5(5)	3(14)	1(8)
Pectoral rays	6(19)	9(30)	9(35)	6(33)	5(16)	2(2)	2(11)	3(19)
Lateral line pored scales	2(3)	4(13)	1(1)	1(14)	4(12)	3(3)	5(21)	4(24)
Rank correlation coefficient within species	0.567		0.683		0.300 [1]		0.800	
Rank correlation coefficient over the four species	0.598							

[1] Rank correlation coefficient=0.783 if Oriental sample is excluded.

DISCUSSION

Meristic variation in fishes apparently has its basis in a number of processes, the relationships between some of which are not clear. Variations in the process of body segmentation during ontogeny are probably the basic source of variation in those counts that may be termed meristic in the strict sense. Vertebrae are laid down relatively early in life and are subject to fewer extraneous influences than meristic characters fixed later in ontogeny. Counts of total vertebrae, therefore, reasonably may be expected

TABLE 5.—*Geographic variation relative to local variation for all hexagrammid species assessed*

[Degree of geographic variation relative to local variation averaged over all characters of each species (see text). Data for total counts column excludes the sectional counts (precaudal and caudal vertebrae; dorsal spines and soft rays). I=index of geographic variation for each species character divided by the corresponding index of local variation] [1]

Species	All counts				Total counts only			
	Σ I	Number characters	Average I	Rank	Σ I	Number characters	Average I	Rank
Oxylebius pictus	10.27	10	1.03	2	5.95	6	0.99	3
Ophiodon elongatus	6.82	9	.76	4	4.52	5	.90	4
Hexagrammos agrammus	3.56	7	.51	7	2.50	5	.50	6
H. otakii	4.96	7	.71	5	4.24	5	.85	5
H. stelleri	5.87	10	.59	6	2.94	6	.49	7
H. octogrammus	2.86	10	.29	8	2.11	6	.35	8
H. lagocephalus [2]	24.09	10	2.41	1	15.22	6	2.54	1
(*H. lagocephalus*) [3]	(8.21)	(10)	(.82)	(3)	(4.69)	(6)	(.78)	(5)
H. decagrammus	9.43	10	.94	3	6.44	6	1.07	2

[1] Arrangement of species-character indices about the median for all indices in a 2 x 8 table indicates that the species distributions are highly unlikely on the basis of chance (chi square=27.4; 99.5 percentile=20.3) and that ranking is justified. Rank correlation analysis between the arrays in the columns all counts and total counts only indicates close correlation (r_s=0.96; 1 percent critical value=0.83). (Tests and confidence levels from Dixon and Massey, 1951.)

[2] All samples.

[3] Oriental sample excluded.

to be the least variable of the meristic characters, a conclusion borne out not only by the hexagrammid variation coefficients (fig. 12) but also by the comparison of hexagrammid coefficients with those for fishes in other families and orders (table 2).

Hubbs (1926) suggested that increased meristic counts in northern representatives of fishes of the northern hemisphere could be caused by dissimilar effects of low temperatures on embryonic rates of growth and differentiation. He theorized that both rates were slowed by lower temperatures but that differentiation was slowed more than growth, with the result that the embryo was larger at the time that differentiation of the counts took place. In later papers Hubbs theorized that a larger number of meristic elements result in the organs of such an embryo because of the greater amount of actual tissue space available when the meristic elements are formed. This explanation is contingent on the assumption that the meristic elements are of roughly the same size in embryos developing at colder temperatures or, as stated by Hubbs and Hubbs (1945, p. 268), "that meristic elements such as vertebrae, scales, and fin rays are laid down at a relatively constant distance apart, in absolute terms, and that the number of elements depends on the space available, up to the time when development stops."

A large number of papers have been published on the subject since Hubbs proposed his theory (for a review see Gordon, 1957), but to my knowledge no one has tested Hubbs' theory by measuring the developing segments in groups of fish embryos that have developed under differing environmental conditions. Another pertinent question is whether meristic variation finds its expression in the entire series of a meristic count or whether it is concerned mainly with variation in the occurrence of terminal elements, as indicated by Hubbs and Hubbs (1945) and McHugh (1950). Ford (1937) believed that variation in the ultimate centra in the vertebral column was the usual cause of variation in vertebral count, but he also cited some examples of variation in vertebrae at the beginning of the column, implying that in some perciform species the centra may be added either at its beginning or at its end. Seymour (1959), however, found nearly equal frequencies of abnormal vertebrae in both caudal and precaudal regions of experimentally reared chinook salmon (*Oncorhynchus tshawytscha*).

The relationship between changes in numerical counts through variation and their changes through evolution should be a fertile field for study. The hexagrammid species form a series in which increase in meristic count parallels habitation of colder waters, both intraspecifically and interspecifically. Neither interspecific increase in vertebral counts through geographic variation nor intraspecific variation in these counts is confined to the posterior region of the vertebral column. It seems likely that several processes, at least, are involved in meristic variation as expressed by vertebral number, and that the addition or loss of vertebrae through the fusion of elements at the ends of the vertebral column may sometimes be but an environment-induced change that takes place when the embryo is not developing under environmental conditions to which the population is genetically adjusted.

It appears that the variation of samples may be of value as an index of the degree to which a population has adapted to local conditions. In two examples, at least, fish populations reared in artificial situations were more variable than those reared in natural situations. In both *Fundulus* *heteroclitus* (table 2) and *Etheostoma exile*,[2] vertebral variation was considerably higher in samples from modified environments than it was in samples of the same or closely related species from natural situations. Further support for the use of variation as an index to adaption may be found in the data of Seymour (1959). Although Seymour did not analyze his data from the standpoint of variation, such an analysis definitely indicates that batches of chinook salmon eggs reared at temperatures above or below those at which the eggs normally develop produce embryos with significantly increased variation in number of vertebrae (fig. 13).

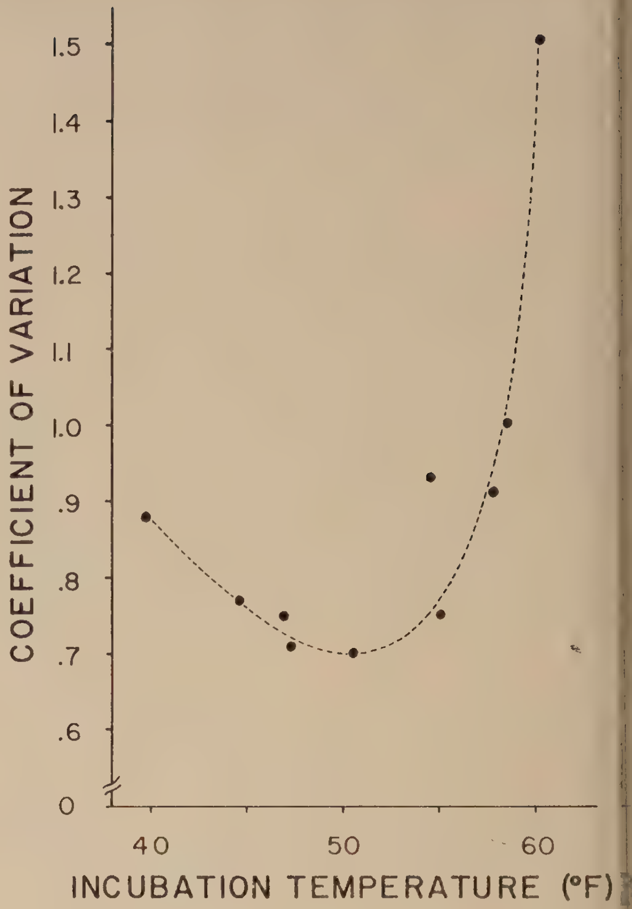

Figure 13.—Vertebral variation in batches of chinook salmon, *Oncorhynchus tshawytscha*, reared at different temperatures. Above and apparently below the middle range of temperatures (from 45° to 55° F.), variation increased markedly in the surviving young. Data fitted by eye. (Calculated from Seymour. 1959.)

In accordance with the large proportion of the data reported in the literature, it appears that the intraspecific geographic variation in the Hexagrammidae is temperature correlated. In general, water temperatures decline northward along the eastern and western coasts of the North Pacific Ocean and are lowest in the Bering Sea and in the Sea of Okhotsk (U.S. Navy Hydrographic Office, 1944). In some eastern temperate coastal regions, particularly off northwest-southeast coastlines and south of projecting headlands, this pattern is disturbed somewhat by the upwelling of colder waters and by the local warming of partly enclosed waters. The geographic variation in the meristic characters of the hexagrammids usually parallels this general geographic gradient in ocean temperatures, and the four species with the most extensive north-south distributions show the largest differences in their counts. Conclusive evidence of temperature-correlated variation in this family is still lacking, however, because little is known about the natural range of temperatures at which hexagrammid eggs develop. At present it only may be surmised that more northerly representatives of the species undergo lower temperatures at sensitive periods of development, such as those described by Tåning (1952). The environmental factors of salinity, oxygen tension, and carbon-dioxide tension, as listed by Gordon (1957), probably can be eliminated as a cause of the variation observed in hexagrammids. Available information indicates that the larvae are pelagic and that juveniles and adults occupy rocky open-coast intertidal and subtidal habitats, both of which probably are quite uniform in salinity and dissolved gases, regardless of latitude. If temperature is proved to be directly or indirectly responsible for much of the intraspecific meristic variation in the Hexagrammidae, its role in the interspecific meristic differences in the family should also be investigated. It is possible that a part of the important meristic differences that characterize hexagrammid species also is due, again directly or indirectly, to the range of temperatures at which a particular species develops.

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[2] Bailey and Gosline (1955) did not refer to the artificial circumstances involved in the rearing of the *Etheostoma exile* population that they cite. These vertebral data are included in a long list of similar data on populations of other percid species that, presumably, were taken in the field. However, the *E. exile* data are the same as those analyzed by Gosline for an earlier paper (1947), and were taken on specimens (called *Poecilichthys exilis* at that time) which had been reared in a hatchery pond that was protected from predators. Gosline stated that the population was possibly not a natural one and that an unusually high percentage of abnormal specimens had been found. The unusually high variation values that I calculated from Gosline's data (table 2) support this supposition.

Geographic variation in the Hexagrammidae differs in at least one important aspect from experimental results reported by Molander and Molander-Swedmark (1957) and Tåning (1952). These authors indicated that for a trout and a flatfish species respectively the means of all meristic counts do not vary in the same direction with higher or lower temperatures. Molander and Molander-Swedmark found that the means of vertebrae are lower in batches of larvae raised at 8° C. than in batches raised at 6° C., which is the opposite of the trend of variation in dorsal ray and anal ray means over this temperature range. Similarly, vertebra and fin ray means vary in opposite directions in Tåning's experiments. In contrast, the direction of geographic variation of these characters in the Hexagrammidae is largely consistent between characters. Similar results are reported by Hubbs and Hubbs[3] in their extensive analysis of geographic variation in the cottid *Leptocottus armatus* in which the means for all meristic counts also decline toward the south. The general trend of geographic variation exemplified by the hexagrammids and *L. armatus* is commonly observed but is not universal. For example, the pattern of geographic variation reported for *Gobius* by Johnsen (1936) shows opposing trends between the means of total dorsal rays and total vertebrae on the one hand and those of pectoral counts and total vertebrae on the other. Such an inverse relationship between the total counts was shown in only one instance among the hexagrammids (pectoral and anal rays in *H. agrammus*), and the relationship may be fortuitous.

Little is known about the causal mechanism behind variation. It appears, however, that numerical characters other than somites and their functionally associated vertebrae probably have at least two sources of variation in addition to those to which vertebrae are subject. On the one hand, these characters follow the vertebrae in time of differentiation, and the formative tissues are therefore susceptible to environmental influence for a greater period of time before the number of elements is fixed. As an extreme example, the number of gill rakers, which appears to be the latest count to be fixed in many fishes (and rakers may continue to be added or lost with growth into adult life), is the most variable numerical character assessed in the Hexagrammidae. On the other hand, variability of a count also seems highly dependent on the anatomical relationships of the elements making up the count. The relationship seems somewhat analogous to the statistical concept of degrees of freedom. The number of vertebral elements corresponds closely to the number of somites and may be described as having but one source of variation (with the somites), or one degree of freedom. The total count of dorsal rays has additional possible sources of freedom in many perciform fishes because elements may be either added or lost at both the anterior and posterior ends of the fin. In the hexagrammid fishes, however, the dorsal fin gains only one degree of freedom over the vertebrae, because the fin spines and their interneurals occupy all available spaces at the insertion of the fin, and the number of spines corresponds closely to the number of anterior interneural spaces. In these fishes there is little opportunity for variation at the fin's anterior insertion. Similarly, the hexagrammids show no variation in addition or loss of fin elements with respect to the number of vertebral elements within the fin (in *Ophiodon elongatus* one element seems to be consistently lacking). The one additional source of variation in number of total dorsal elements over number of vertebrae in these fishes lies in the addition or deletion of elements at the posterior end of the fin. The total elements in the dorsal fin of hexagrammids thus may be characterized as having two degrees of freedom. Because of the variable fate of adjoining rays separating the spinous and soft portions, the spinous dorsal fin of these fishes also has two degrees of freedom. The soft-rayed fin, however, like the anal fin, probably is able to gain or lose elements at either end, and thus may be characterized as having three degrees of freedom.

Hubbs and Hubbs (1945) held that the pectoral rays vary entirely at the lower part of the fin in *L. armatus*. Carl L. Hubbs states (personal communication, 1961), "I believe that it is usually not true that elements may be added at both ends, as in the dorsal and anal. It does seem that this does occur in the first dorsal of darters (as *E. exile*), in which the front of the fin slopes down, with no specialized elements . . . . But usually the front ray(s) is (are) specialized and fixed as in an anal fin with I, II, or III spines (depending on the species) or in the pectoral fin with the uppermost ray specialized (one short; the next long, thick, unbranched). The anal fin is usually fixed in front of the posterior of the anus and by vertebral connections." He adds. "If the variation in pectoral rays was at either end, then it wouldn't be the almost universal rule that the lowest (i.e., morphologically most posterior) ray is the shorter on the side with the higher number of rays." However, an unstable forward position of a fin's anterior formative tissue may have little to do with the later formation of the specialized anterior fin elements, which merely will appear one or more somites removed from their usual position. The insertions of dorsal and anal fins certainly have changed materially in the evolution of the various perciform fishes; a strong argument that the somites of insertion are subject to variation as well as the other morphological characteristics of fishes. Furthermore, specialized elements such as anal fin spines do vary in number in some perciform fishes, in eight of nine hexagrammid species, for example, anal spines vary over two or three units. Also, the variation in the number of the first vertebral element bearing the first haemal spine (presumably one cause of reciprocal variation in numbers of precaudal and caudal vertebrae) argues against the specialized anterior portion of the anal fin being fixed completely serially in respect to the vertebral column. Although Hubbs' argument concerning the last element in the pectoral fins seems persuasive, it applies mainly to the length of the formative tissue at the time of meristic differentiation and may have little to do with whether the formative tissue is shifted forward or backward one or two somites or whether the tissue is "longer" because the tissue for additional elements is added anteriorly, posteriorly, or medially.

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[3] Hubbs, Carl L., and L. C. Hubbs. Analysis of meristic variation in *Leptocottus armatus*, a fish of western North America. Manuscript being prepared for publication, Scripps Institution of Oceanography, La Jolla, Calif.

The methods of variation study utilized in my paper are admittedly crude in comparison with refinements that would have been possible were the study more limited in scope and more specimens available. It is evident from the data presented that the variation in samples is influenced by the type of sample chosen and that a hierarchy of values may be constructed from data obtained by different sampling methods. If geographic variation occurs, it is the same as saying that the value for the variation of all samples of a character, when lumped, is greater than the variation in regional samples, which, in turn, should exceed that of local samples. Local samples should be less variable than regional assortments because the geographic component of variation should decrease as the samples are limited to a narrower geographic range. Theoretically, further reduction of variation by more restrictive sampling is possible. Local samples drawn from a single year class should reduce the amount of variation over samples drawn from several year classes, especially where environmental conditions change appreciably from year to year. In a single instance o this type available among the hexagrammids, a large sample of a single year class of *Ophiodon elongatus* from San Francisco Bay (figs. 2 to 11) yielded considerably lower values for variation in most of its meristic elements than mixed samples taken elsewhere along the species range.[4] Even further reductions in the variation of samples may occur with more selective sampling. Significant differences between meristic counts in samples of a year class taken from individuals spawned early and late in the spawning season have been reported for numerous fishes from both fresh-water habitats (Hubbs, 1922 and 1924) and salt-water habitats (Hubbs, 1925, and Hubbs and Hubbs, 1954). Even the variation in a sample of fish spawned at the same time and place may be lessened. Motley (1934 and 1937) demonstrated lower values for variation in samples of siblings of *Salmo* spp. than in samples of a single year class from mixed parentage. In conclusion, because of this hierarchy of values for character variation that depends on the type of sample chosen, it is important that the sampling method be kept in mind when comparisons of variation are being made.

It is difficult to assess what relationship, if any, exists between the number of lateral line pored scales and the number of somites; and the hexagrammids are not analyzed in this regard. Scales are laid down late in ontogeny, and their number is subject to an undetermined set of influences after the fixation time of the somites, with the result that nearly all mechanical correspondence between the two meristic series, such as that described for fin rays and vertebrae, may be lost.

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[4] However, the year-class differences in variation are nearly restricted to the characters that also show geographic variation (dorsal spines, dorsal soft rays, total dorsal rays, and total anal rays). This adds weight to the foregoing observations concerning a positive relationship between local and geographic variation.

SUMMARY AND CONCLUSIONS

The following conclusions are based on all available samples of the species. While the specimens are numerous in the aggregate, some samples were necessarily small and inadequate for conclusive testing of the hypotheses. Therefore these are provisional conclusions that must await intensive examination of large series of specimens for final substantiation.

1. There is significant geographic variation in the means of some meristic counts in all eight of the hexagrammid species investigated.
2. The species differ in the number of meristic characters that vary geographically; even similar species differ in this respect in overlapping portions of their geographic ranges.
3. Geographic variation in meristic counts probably is related directly or indirectly to environmental temperatures over the geographic ranges.
4. Geographic variation in the number of gill rakers does not appear to be correlated with the variation of those characters associated with the body somites.
5. The variation shown by meristic characters is remarkably consistent for each character, not only for the different regions occupied by a single species but also between the eight hexagrammid species studied.
6. Meristic variation in the Hexagrammidae usually is as low as or lower than that calculated from the data for other fishes randomly selected from the literature.
7. Despite the general consistency of variation shown by each character within and between hexagrammid species, two species differ significantly in overall variation (as measured by the coefficient of variation) from the family averages. The most primitive representative, *Oxylebius pictus*, generally is the most variable, whereas the highly specialized *Hexagrammos decagrammus* is less variable than the average of species of the family in 13 out of 15 characters. However, no other examples of correlation were found between overall variation in the hexagrammid species and subjective estimates of their specializations.
8. In species exhibiting marked geographic variation, the variation of different meristic characters within regional samples is positively correlated with the degree of geographic variation.
9. The coefficient of variation may be of some value in assessing how well fish populations are adapted to environmental conditions during embryonic stages.
10. The hypothesis is presented that both the time of fixation and the structural relations of the meristic parts are operative in creating differences in variation in meristic characters.

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LITERATURE CITED

Bader, Robert S.
1955. Variability and evolutionary rate in the oreodonts. Evolution, vol. 9, No. 2, pp. 119–140.

Bailey, Reeve M., and William A. Gosline.
1955. Variation and systematic significance of vertebral counts in the American fishes of the Percidae. University of Michigan, Ann Harbor, Museum of Zoology, Miscellaneous Publication 93, 44 pp.

Brown, Jerram L.
1958. Geographic variation in southeastern populations of the cyprinodont fish, *Fundulus notti* (Agassiz). American Midland Naturalist, vol. 59, No. 2, pp. 477–488.

Crawford, Ronald W.
1956. A study of the distribution and taxonomy of the percid fish, *Percina nigrofasciata* (Agassiz). Tulane University, New Orleans, Tulane Studies in Zoology, vol. 4, No. 1, 55 pp.

Dixon, Wilfrid J., and Frank J. Massey, Jr.
1951. Introduction to statistical analysis. McGraw-Hill Book Company, Inc., New York, 370 pp.

Ford, E.
1937. Vertebral variation in teleostean fishes. Journal of Marine Biological Association of the United Kingdom, vol. 22, No. 1, 60 pp.

Gabriel, Mordecai L.
1944. Factors affecting the number and form of vertebrae in *Fundulus heteroclitus*. Journal of Experimental Zoology, vol. 95, No. 1, pp. 105–147.

GIBBS, ROBERT H., JR.

1957a. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. II. Distribution and variation of *Notropis spilopterus*, with the description of a new subspecies. Lloydia, vol. 20, No. 3, pp. 186–211.

1957b. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. III. Variation and subspecies of *Notropis venustus* (Girard). Tulane University, New Orleans, Tulane Studies in Zoology, vol. 5, No. 8, pp. 175–203.

GORDON, MYRON.

1957. Physiological genetics of fishes. *In* the physiology of fishes. Margaret E. Brown (editor), vol. 2. Academic Press, New York, 526 pp.

GOSLINE, WILLIAM A.

1947. Some meristic characters in a population of the fish *Poecilichthys exilis:* their variation and correlation. University of Michigan, Ann Arbor, Museum of Zoology, Occasional Papers, No. 500, 23 pp.

HUBBS, CARL L.

1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of water during development. American Naturalist, vol. 56 (July-August), pp. 360–372.

1924. Seasonal variation in the number of vertebrae of fishes. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 2 (1922), pp. 207–214.

1925. Racial and seasonal variation in the Pacific herring, California sardine and California anchovy. State of California Fish and Game Commission, Fish Bulletin No. 8, 23 pp.

1926. The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. American Naturalist, vol. 60 (January-February), pp. 57–81.

HUBBS, CARL L., AND LAURA C. HUBBS.

1945. Bilateral asymmetry and bilateral variation in fishes. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 30, 310 pp.

1954. Data on the life history, variation, ecology, and relationships of the kelp perch, *Brachyistius frenatus*, an embiotocid fish of the Californias. California Fish and Game, vol. 40, No. 2, pp. 183–198.

HUBBS, CARL L., AND KARL F. LAGLER.

1949. Fishes of the Great Lakes region. Cranbrook Institute of Science, Bloomfield Hills, Mich., 186 pp.

JOHNSEN, SIGURD.

1936. On the variation of fishes in relation to environment. Bergens Museums Årbok Naturvidenskapelig Rekke, 4 hefte, 26 pp.

MATSUBARA, KIYOMATSU.

1943. Studies on the scorpaenoid fishes of Japan (II). Transactions of Sigenkagaku Kenkyusyo, No. 2, pp. 171–486.

MCHUGH, JOHN L.

1950. Variations and populations in the clupeoid fishes of the North Pacific. Ph.D. Thesis, University of California at Los Angeles, 116 pp.

MOLANDER, ARVID R., AND MARTHA MOLANDER SWEDMARK.

1957. Experimental investigations on variation i plaice (*Pleuronectes platessa* Linne). Reports Lysekil Institute of Marine Research (Biology) No. 7 44 pp.

MOTTLEY, C. MCC.

1934. The effect of temperature during developmen on the number of scales in the Kamloops trout *Salmo kamloops* Jordan. Contributions to Canadian Biology and Fisheries (A, general, No. 41) vol. 41, No. 8, pp. 255–263.

1937. The number of vertebrae in trout (*Salmo*) Journal of Biological Board of Canada, vol. 3 No. 3, pp. 169–176.

PRASAD, RAGHU R.

1958. Racial analysis of *Clevelandia ios* (Jordan an Gilbert) in California waters. American Midlan Naturalist, vol. 59, No. 2, pp. 465–476.

QUAST, JAY C.

1960. The fishes of the family Hexagrammidae: thei classification, variation, and osteology. Ph.D. Thesis, University of California at Los Angeles, 380 pp.

RANDALL, JOHN E.

1955. A revision of the surgeon fish genus *Ctenochaetus*, family Acanthuridae, with descriptions of five new species. Zoologica, vol. 40, part 4, pp. 149–166.

1956. A revision of the surgeon fish genus *Acanthurus*. Pacific Science, vol. 10, No. 2, pp. 159–235.

RANEY, EDWARD C.

1957. Subpopulations of the striped bass, *Roccus saxatilis* (Walbaum), in tributaries of Chesapeake Bay. *In* U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries, John C. Marr (editor), No. 208, pp. 85–107.

SCHMIDT, P. U.

1950. Fishes of the Sea of Okhotsk. Akademiia Nauk, SSSR, Moscow, 370 pp.

SEYMOUR, ALLYN.

1959. Effects of temperature upon the formation of vertebrae and fin rays in young chinook salmon. Transactions of the American Fisheries Society, vol. 88, No. 1, pp. 58–69.

SIMPSON, GEORGE GAYLORD.

1953. The major features of evolution. Columbia University Press, New York, 434 pp.

SIMPSON, GEORGE GAYLORD, ANNE ROE, AND RICHARD D. LEWONTIN.

1960. Quantitative zoology. Harcourt, Brace and Company, Burlingame, New York, 440 pp. [Revised edition.]

STRASBURG, DONALD W.

1955. North-south differentiation of blenniid fishes in the central Pacific. Pacific Science, vol. 9, No. 3, pp. 297–303.

TÅNING, Å. VEDEL.
1952. Experimental study of meristic characters in fishes. Biological Reviews of the Cambridge Philosophical Society, vol. 27, No. 2, pp. 169–193.

TAYLOR, FREDERICK H. C.
1957. Variations and populations of four species of Pacific Coast flatfish. Ph.D. Thesis, University of California at Los Angeles, 351 pp.

UNITED STATES NAVY HYDROGRAPHIC OFFICE.
1944. World atlas of sea surface temperatures. Publication 225, 2d edition.

MOVEMENTS, GROWTH, AND RATE OF RECAPTURE OF WHITEFISH TAGGED IN THE APOSTLE ISLANDS AREA OF LAKE SUPERIOR

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ABSTRACT

A total of 1,303 whitefish were marked with spaghetti streamer tags in Wisconsin waters of Lake Superior in November of 1959, 1960, and 1961 and June–July 1960. The fish tagged in June–July 1960 were mostly undersized (less than 17 inches long) whereas those captured on the spawning grounds and tagged in November 1959–61 were almost all legal size. Of the 374 recoveries (28.7 percent), nearly all were made during the first 2 years after tagging. The earliest returns were from fish which were among the largest when tagged. Over one-half of the recoveries were made within 5 miles of the tagging site; the greatest distance traveled by an individual was 25 miles. The fish tagged in June–July 1960 grew 1.6 inches the first season and 1.2 the second. Of 27 whitefish recaptured within 6 months from the November 1959–61 group, 17 (63 percent) had lost length (range from decrease 0.1 to 1.4 inches). Whitefish of the June–July group recaptured during the second growing season after tagging gave an exploitation rate of 22.6 percent. First-year returns from the November 1959–61 tagging gave an exploitation rate of 20.5 percent. The true exploitation rate probably is higher since no allowance has been made for tagging mortality, loss of tags, or unreported recaptures.

The production of whitefish, *Coregonus clupeaformis* (Mitchill), in the U.S. waters of Lake Superior declined from over 4½ million pounds in 1885 to 113,000 pounds in 1913, the lowest production recorded. Since 1913 the catch has fluctuated widely; the take exceeded 1 million pounds in 1948–50 and 1954–55 but dropped to 284,000 pounds in 1960.

The production of whitefish in Wisconsin waters of Lake Superior has contributed about 35 percent to the total U.S. output in the lake over the past 50 years. The Apostle Islands region provides nearly all of Wisconsin's production.

The progressive decline of the lake trout (*Salvelinus namaycush*) since 1955, followed by the complete closure of the lake trout fishery in 1962, has made the whitefish of increased importance to the economy of Wisconsin commercial fishermen. Sound management and rational exploitation should be based on a thorough knowledge of the species. The present paper is a contribution to this knowledge.

The first tagging study of whitefish in Lake Superior was in 1951 when staff members of the Fish and Wildlife Service marked 208 undersized (then less than 2 pounds) whitefish with nylon-streamer tags off Bete Grise, Mich. Only 23 fish (11 percent) were recaptured, all within 2 months after tagging. Except for one fish which had traveled 40 miles, all recoveries were made within 20 miles of the tagging site.

In 1955–59, the Wisconsin Conservation Department tagged 2,400 whitefish in the Apostle Islands region. Only 78 recoveries (3.3 percent) were reported, nearly all within 1 year after tagging. All of the recaptured fish were reported from the Apostle Islands region.

The limited recovery of the whitefish tagged by Wisconsin personnel was believed to reflect a high rate of tag loss. The tag used in this earlier experiment was a streamer-type attached to the

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body of the fish posterior to the dorsal fin. Nylon thread (No. 69 Nyloc) was used in 1955–57, and polyethylene thread was used in 1958–59. The difference between the percentage returns of tags held by the two types of thread was negligible.

Evidence that these types of tags are lost was given by Eschmeyer (1959), who found that only 1 of 200 streamer tags attached to lake trout with No. 34 or 46 nylon thread remained intact at the end of 1 year. Budd (1957) estimated that the loss of streamer tags on whitefish tagged in South Bay (Lake Huron), Ontario, was about 10 percent per year.

The present study is an extension of the earlier work of the Wisconsin Conservation Department. We wished to learn more about the migratory habits, growth, and exploitation rate of the Apostle Islands whitefish.

MATERIALS AND METHODS

A total of 1,303 whitefish were tagged in the Apostle Islands area during November 1959–61

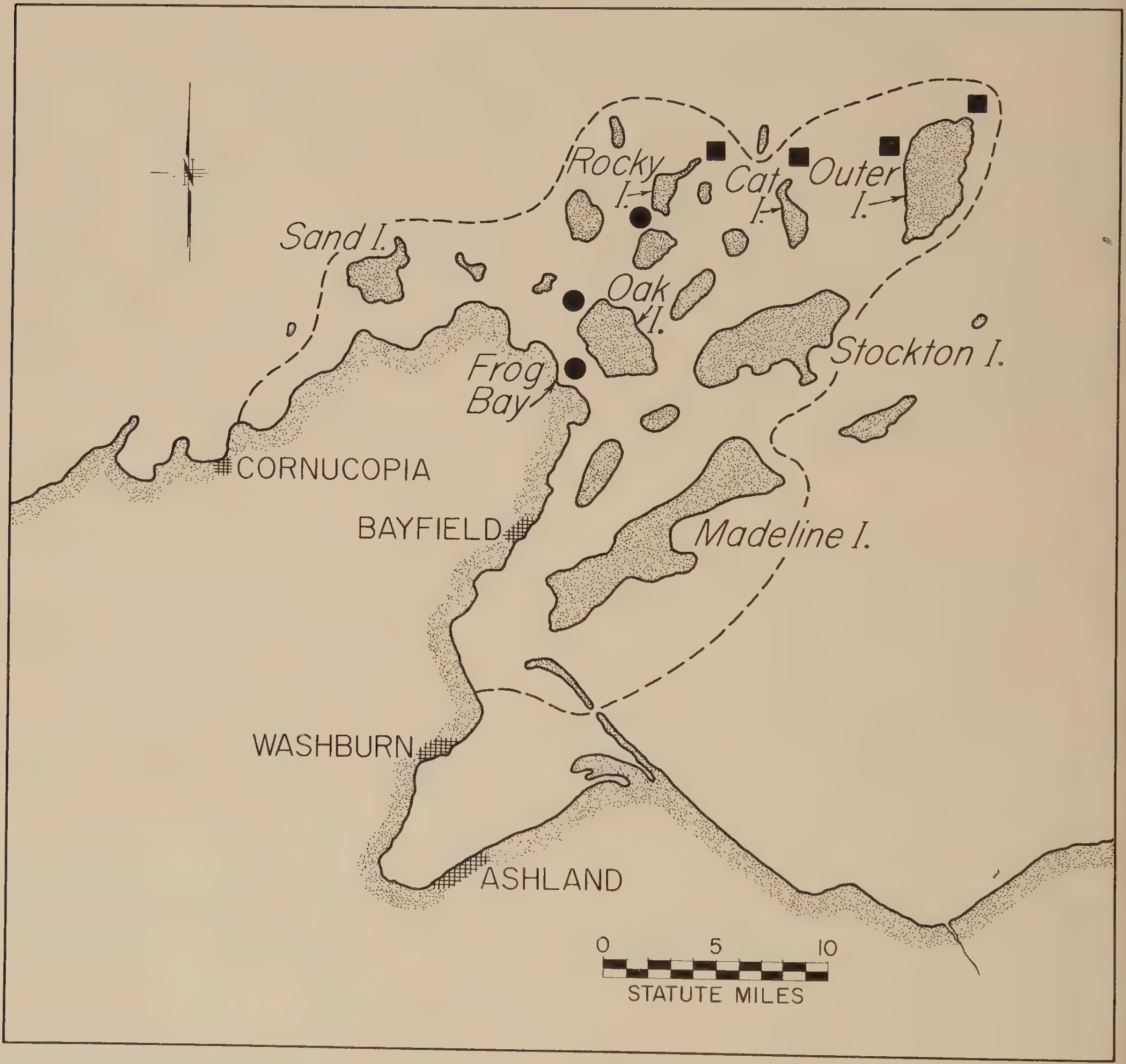

FIGURE 1.—Apostle Islands region of Lake Superior. The dots represent locations where whitefish were tagged in June–July 1960 and the squares show locations of the November 1959–61 tagging. All recoveries were made within the dotted line.

TABLE 1.—*Number of whitefish tagged in the Apostle Islands region according to location and date, and the number and percentage of recaptures from each tagging, 1959–61*

Item	Tagging locality						Length when tagged	
	Rocky Island	Oak Island	Frog Bay	Cat Island	Outer Island	All locations	Average	Range
June–July 1960:								
Number tagged	455	563	104	-------	-------	1,122	*Inches* 15.4	*Inches* 10.6–17.4
Number recaptured	139	169	21	-------	-------	329	------	-------
Percentage recaptured	30.5	30.1	20.2	-------	-------	29.3	------	-------
November 1959–61:								
Number tagged	73	-------	------	96	12	181	18.8	16.0–23.7
Number recaptured	20	-------	------	20	5	45	------	-------
Percentage recaptured	27.4	-------	-----	20.8	41.7	24.9	------	------
All dates:								
Number tagged	528	563	104	96	12	1,303	15.9	10.6–23.7
Number recaptured	159	169	21	20	5	374	------	-------
Percentage recaptured	30.1	30.0	20.2	20.8	41.7	28.7	------	-------

and June–July 1960 (table 1, fig. 1). The 1,122 fish tagged in June–July 1960 were collected in commercial pound nets (50–70 feet deep, 4¾-inch-mesh pot); the remaining 181 whitefish came from large-mesh gill nets (from 4½- to 5½-inch mesh) fished on the whitefish spawning grounds from the Bureau of Commercial Fisheries research vessel *Siscowet*. One purpose of tagging spawning-run fish was to detect possible "homing" behavior.

The tag—a spaghetti streamer—used in this experiment was a modification of the type used by Wilson (1953) for marking tuna. It consisted of a vinyl plastic tube (outside diameter, 0.094 inch) with a yellow plastic disc attached to one end. A stainless steel tube served as a needle for piercing the back of the fish just posterior to the dorsal fin. The tubing was placed inside the steel needle; as the needle passed through the fish, the tag was carried through with it. The ends of the plastic tubing were joined by a small metal clamp, similar to a bird band. No reward was offered for the return of the tags. Although the inscription on the plastic disc instructed that the tags be forwarded to the Bureau's Biological Laboratory in Ann Arbor, Mich., most were sent directly to the field station at Ashland, Wis.

The whitefish tagged from pound nets in the summer of 1960 ranged from 10.6 to 17.4 inches long (average, 15.4 inches). The spawning-run fish tagged aboard the *Siscowet* were considerably larger (16.0–23.7 inches; average, 18.8 inches).

Most of the returns (296) came from the intensive summer pound net fishery, and the remainder (78) from large-mesh gill nets fished under the ice during the winter. The percentage of recoveries from the various tagging locations and dates varied little. Among groups of 40 or more fish tagged at one location, the percentage return ranged from 20.2 to 30.5. The total percentage return was 28.7 for all tagging combined.

The number of tag returns used for various phases of this study varies according to the information received with the tags. Complete data, i.e., date and location of capture and length of the fish were reported with most of the returns. Some reports, however, were incomplete and their usefulness was limited according to the information received. Because reports of recoveries declined sharply in the summer of 1962 the study was terminated December 31, 1962. I felt that the few additional returns that might be reported after this date would not influence the results appreciably.

TIME BETWEEN TAGGING AND RECOVERY

The time between tagging and recovery for Apostle Islands whitefish was influenced by seasonal fishing pressure and by the size of the fish when tagged. The recaptures from the group tagged in June–July 1960 were highest during the summer pound net fishery of 1961. Since whitefish tagged in June–July 1960 were mostly undersized and returned to the lake if captured, returns from them were few during the first several months out.

The percentage of whitefish recaptured from the June–July 1960 group (table 2) increased from 6.3 percent during the first 10 months (July–April) to 19.8 percent during the 11- to 22-month (May–April) period. The cumulative percentage recovered was 26.1 percent at the end of 22 months, only 3.3 percent below the final percentage (29.4 percent) at the end of 29 months. Of the 37 recoveries made after 22 months, only 4 were reported later than 24 months. The percentage of the total number recaptured was also highest (67.3 percent) during the 11- to 22-month period and the cumulative percentage of the total stood at 88.8 percent at the end of 22 months.

Table 2.—*Recoveries of whitefish tagged in June–July 1960 according to length of time at liberty*

Item	Time out (months)		
	<11	11–22	23–29
Number recaptured	71	222	37
Percentage recaptured	6.3	19.8	3.3
Cumulative percentage	6.3	26.1	29.4
Percentage of total recoveries	21.5	67.3	11.2
Cumulative percentage	21.5	88.8	100.0

Of the 43 returns from fish tagged during the fall spawning season (November) in 1959–61 (table 3), all but 5 were reported during the first 12 months (20 were taken during the first 5 months in the winter fishery, and 18 in the following 12 months). No recoveries were made after 20 months. The cumulative percentage of recapture was 20.9 percent at the end of 12 months, only 2.8 percent below the total percentage return of 23.7. The percentage of the total recaptured was highest during the first 5 months, and the cumulative percentage stood at 88.4 percent at the end of 12 months.

The small number of returns after the first year for fish tagged in November 1959–61 and after the second year for the June–July 1960 group suggests either a high rate of tag loss or a heavy natural mortality.

DISTANCES TRAVELED

The distances traveled by tagged whitefish were relatively small regardless of the time between tagging and recapture. Of the small whitefish tagged in June–July 1960, 142 fish (64.6 percent of the total recoveries) were recaptured at distances less than 5 miles from the tagging site (table 4). Only 19 fish (8.6 percent) had traveled more than 10 miles, and the greatest distance traveled by an individual was 17 miles.

More than half (56.5 percent) of the recoveries of the larger whitefish tagged during the fall spawning seasons were within 5 miles of the tagging site, but 26.1 percent (6 fish) traveled more than 10 miles. The greatest distance traveled by a whitefish tagged during the spawning run was 25 miles. The *Siscowet* recovered only one whitefish which had returned to spawn on the same grounds where it was tagged.[1]

Table 3.—*Recoveries of whitefish tagged in Novembe 1959–61 according to length of time at liberty*

Item	Time out (months)		
	<6	6-12	>12
Number recaptured	20	18	
Percentage recaptured	11.0	9.9	2.
Cumulative percentage	11.0	20.9	23.
Percentage of total recoveries	46.5	41.9	11.
Cumulative percentage	46.5	88.4	100.

Table 4.—*Recoveries of tagged whitefish according t distance traveled from tagging site*

Tagging period and item	Distance traveled (miles)			
	<5	5–10	>10	Greatest distance
June–July 1960:				
Number recaptured	142	59	19	1
Percentage of total recaptures	64.6	26.8	8.6	--------
Cumulative percentage	64.6	91.4	100.0	--------
November 1959–61:				
Number recaptured	13	4	6	2
Percentage of total recaptures	56.5	17.4	26.1	--------
Cumulative percentage	56.5	73.9	100.0	--------

Since the major portion of the pound net fishery in the Apostle Islands is concentrated within a 20-mile radius of Bayfield, Wis., it was to be expected that most of the recoveries would come from that area. Gill nets, on the other hand, are fished along the entire south shore of Lake Superior. Had the whitefish migrated greater distances, recoveries should have been made outside the Apostle Islands region.

The lack of recoveries from outside the Apostle Islands region supports Dryer's (1963) suggestion, based on growth data, that the whitefish in the Bayfield region are one of a number of distinct stocks in Lake Superior. These stocks of fish have characteristic growth rates (Apostle Islands and Munising Bay stocks grow extremely slowly in comparison with those from Marquette and Whitefish Bay).

Smith and Van Oosten (1940) reported that of 101 returns from 457 whitefish tagged in Lake Michigan, only 4 were recovered at distances greater than 25 miles. They further indicated that no correlation could be found between distances traveled and time out. Budd (1957) reported that one whitefish had traveled 150 miles from the tagging site in South Bay, Lake Huron. His tag returns suggested, however, that the South Bay stock retains its identity and that fish return to South Bay during the winter or early spring.

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[1] Since the completion of this report the Wisconsin Conservation Department has given me records of the recapture in 1963 of six whitefish from the spawning grounds on which they were tagged.

It is, of course, impossible to determine the distance traveled before an individual was recaptured. A whitefish recaptured 2 years after tagging at a point only 5 miles from the tagging site certainly could have moved extensively at some time during the 2-year interval.

GROWTH OF TAGGED WHITEFISH

The data on growth in length of tagged whitefish are summarized according to group of fish tagged and the number of growing seasons completed before recapture. Since the growth rates and recapture dates for whitefish tagged in June–July 1960 differed from those for fish tagged during the November spawning season in 1959–61, the two groups are kept separate for the discussion of growth in length.

The number of growing seasons completed for recaptured whitefish was determined as follows: fish from the June–July 1960 group which were recovered during the following November–June (5–12 months out) were considered to have completed 1 growing season; those fish which were out 17–24 months after tagging had completed 2 growing seasons. Since annulus formation occurs n mid-June for Lake Superior whitefish (Dryer, 1963), some of the fish conceivably may have completed a small amount of the current season's growth before they were tagged. This small growth, if any occurred, should not seriously mpair the data on the first year's growth.

The estimates of growth of individual whitefish are the differences between lengths at recapture reported by commercial fishermen and lengths at tagging, measured by staff members. The measurements at tagging may be considered accurate within the normal limits of error common to field operations. The dependability of measurements by commercial fishermen doubtless varies from ndividual to individual. Many fishermen do not carry a ruler or yardstick but have a board with a mark at 17 inches, the minimum legal length for both whitefish and lake trout. The distance between this mark and the end of the tail probably was estimated for many fish to obtain the reported ength. Other fish probably were measured closely. The fishermen's measurements must be ecognized as less accurate than the measurements at tagging but they give a reasonably dependable estimate of average if not of individual growth.

Growth was relatively slow for the whitefish recaptured from those tagged in June–July 1960 (table 5). The increments ranged from −1.4 to 3.9 inches for fish recaptured after 1 year and from 0.9 to 7.4 inches for those recaptured after 2 growing seasons. The average increment of length was 1.6 inches for fish out 1 growing season and 2.8 inches for those out 2 growing seasons.

Since most of the whitefish tagged in June–July 1960 were undersized (average length, 15.4 inches), few returns from them were expected until they reached the legal size of 17 inches.[2] It was expected further that the first returns would come from the larger fish since they would be the first to reach legal size. The average length at tagging was 15.9 inches for fish out 5–10 months, 15.5 inches for those out 12 months, and 15.1 inches for those out 24 months. Smith and Van Oosten (1940) also found that the first recoveries of tagged whitefish in Lake Michigan were from fish which were among the largest when tagged.

TABLE 5.—*Distribution of length increments of tagged whitefish recovered in the Apostle Islands region by time tagged and number of growing seasons.*

Increment of total length	Period of tagging and number of growing seasons		
	June–July 1960		November 1959–61
	1 season	2 seasons	<1 season
Inches			
7.0–7.4		1	
5.0–5.4		1	
4.5–4.9		2	
4.0–4.4		3	
3.5–3.9	1	3	
3.0–3.4	2	4	
2.5–2.9	16	2	
2.0–2.4	33	10	
1.5-1.9	67	4	
1.0-1.4	56	5	1
.5–.9	23	2	1
.1–.4	4		4
0. 0	1		4
−.1 −.4	1		10
−.5–−.9	2		6
−.1–−1.4	1		1
Number of fish	207	37	27
Average length when tagged	15. 7	15. 2	18. 6
Average length when recaptured	17. 3	18. 0	18. 5
Average increment	1. 6	2. 8	−. 1

Nearly all of the recoveries (for which length data are available) from fish tagged in November 1959–61 were made before the start of the following growing season (less than 8 months out). Many of the spawning-run whitefish recaptured during the following December–June showed a loss of length. Of the 27 whitefish recaptured, 17 (63 percent) had lost length (range, from —.1 to —1.4 inches) and 4 had the same length as at tagging. Six of the fish put on growth over the winter; the largest increase was 1.4 inches. Only 4 fish for which appropriate data are available were taken after completion of 1 growing season. The average growth for these fish was 0.9 inch (range, 0.3–2.5 inches).

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[2] Fishermen reported releasing many undersized tagged whitefish from their pound nets during the summer of 1960.

Carbine and Applegate (1948) reported that 50 percent of the tagged northern pike (*Esox lucius*) recovered by anglers from Houghton Lake and Muskegon River, Mich., showed "negative growth." They considered the data erroneous and excluded them from their discussion of growth. Eschmeyer and Jones (1941) also found that fish recaptured soon after tagging in Norris Reservoir, Tenn., often had lost several millimeters in length.

Some animals can, of course, lose considerable length. Sea lampreys with their cartilaginous skeleton, for example, shrink considerably between December and the following spring (Parker and Lennon, 1956). Shrinkage offers a more difficult problem for those organisms which have an osseous axial skeleton; any loss of length of necessity is accommodated by a reduction in the distance between the successive vertebrae. Also to be considered in the apparent shrinkage in length is whether or not the fish is alive at the time of measurement after recapture. Measurements made several hours after recapture would undoubtedly reflect the normal shrinkage which occurs after death. Shetter (1936b) found that brook trout shrink about 2.6 percent due to rigor mortis.

Little doubt exists that the growth rate of fish is retarded by tags. The extent of retardation in growth depends on such factors as type of tag, location of the tag on the fish, and the species of fish tagged. Eschmeyer and Crowe (1955) reported that the annual length increments of walleyes bearing jaw tags averaged less than two-thirds those of untagged fish. Smith, Krefting, and Butler (1952) determined that walleyes bearing jaw tags had not formed an annulus in 2 years after tagging and that growth was negligible. Eschmeyer (1959) stated that the growth of lake trout in a rearing pond was retarded about 25 percent when the fish were tagged with Petersen, cheek, and lower-jaw tags.

EXPLOITATION RATE

Estimates of exploitation rates based on tagging studies may be prejudiced by various factors The principal difficulties originate in four majo sources of bias: loss of tags; tagging mortality unreported returns; and increased vulnerability of tagged fish to fishing gear.

The first three sources of bias lead to underestimates of exploitation rates, and bias through increased vulnerability of tagged fish to fishing gear leads to overestimates. When estimates are based on the ratio of the number of fish returned to the number tagged, it is assumed implicitly that all of the tags remained intact that all of the recaptures were reported, and that tagging did not cause mortality or increase vulnerability.

Tag loss and mortality from tagging are probably the most serious deterrents to the quantitative interpretation of data from any tagging study. Various experiments (Snyder, 1932 Markus, 1933; Shetter, 1936a; and Eschmeyer 1959) have revealed losses with various types of tags ranging from 40 to 100 percent within 1 year after tagging. Data are not available on the percentage loss of the spaghetti tags used in this study but I believe it is less than that for jaw and streamer tags.

The extent of mortality caused by tagging depends on the type of tag, the hardiness of the species tagged, the condition of the fish at tagging the method of handling the fish during tagging and probably on other factors as well. Eschmeyer (1959) lost only 9 lake trout of 600 held in a rearing pond and tagged with Petersen cheek, jaw, and streamer tags. The mortality of whitefish tagged with spaghetti tags is unknown

No method exists for judging the number of tagged fish recaptured but not reported. Most fishermen intend to report tagged fish but sometimes, through neglect, they forget ,to return the tag. A few deliberately withhold information on tag returns.

Information is lacking also on the effect of the tag on the vulnerability of the whitefish to commercial gear. Buettner (1961) found that returns from lake trout tagged with Petersen tags were 2.6 times greater than those from fish bearing tags of other types. He concluded that the high rate of returns of Petersen-tagged fish was due to entanglement of the tags in the webbing of the gill nets. Eschmeyer, Daly, and Erkkila (1953) also suggested that fish tagged with Petersen tags were far more vulnerable to the fishery than were fish bearing other types of tags. The relative vulnerability of fish tagged with these other types of tags is not fully known, but it seems reasonable to assume that the presence of any external tag would increase the chance of capture in certain gears, particularly gill nets.

The effect of the increased vulnerability of the tagged whitefish to the fishing gear may not be great in this study since nearly all (92 percent) of the returns of fish used for inquiry into exploitation rates came from pound nets. The heavy twine of pound nets rarely gills or otherwise entangles whitefish. Tags may, nevertheless, cause pound nets to hold a few fish that otherwise might slip through the meshes.

Even though the effect upon the data from loss of tags, unreported returns, and tagging mortality may be offset in some measure by compensating increased vulnerability of tagged fish to the fishing gear, I believe that the compensation was only partial and that data on exploitation rate offered later in this section are in fact underestimates—possibly severe ones. I have not, however, undertaken any arbitrary adjustment such as that of Smith and Van Oosten (1940) who based their estimation of fishing intensity on various species in Lake Michigan on the assumption that 50 percent of the fish had lost their tags.

Since nearly all of the 1,122 whitefish tagged in June–July 1960 were undersized at tagging, the first-year returns were so few that the rate of exploitation for them could not be estimated over the first year of freedom. The rate of exploitation was estimated from second-year returns, however, by the following procedure: the average growth in length of the tagged whitefish recaptured after completion of 1 growing season (1.6 inches—table 5) was added to each of the lengths of whitefish tagged in June–July 1960 to determine the number of tagged fish that would have reached legal size at the beginning of the second fishing season (May 1, 1961); the number of fish which would have reached legal size at the beginning of the second year (737) was reduced by 59, the number taken as legal-size fish during the first year of freedom, to obtain the adjusted number of 678 actually available; the 153 fish recaptured during the second growing season gave an estimated exploitation rate of $100\times\frac{153}{678}$ or 22.6 percent.

The rate of exploitation for Apostle Islands whitefish was also estimated from first-year returns of the legal-size fish tagged in November 1959–61. Of the 171 legal-size fish tagged, 35 (20.5 percent) were recaptured during the following 12 months (December–November) after tagging.

The close agreement between estimates of exploitation rates of the November 1959–61 fish (20.5 percent) and the June–July 1960 group (22.6 percent) strongly suggests that the system for estimation of the exploitation rate of the latter group was reasonably sound.

Annual exploitation rates a little above 20 percent cannot be termed excessive. These estimates almost surely are minimal, and as was brought out in earlier discussions, they may be far below the true value. Strong evidence of extremely heavy exploitation of whitefish in the Apostle Islands area was given by Dryer (1963), who found that the intensive summer pound net fishery selected the legal-size whitefish from the population early in the season, leaving mostly the undersized, slowly growing members of an age group during late season. The average size of the age groups declined progressively through the summer.

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LITERATURE CITED

Budd, John.
1957. Movements of tagged whitefish in northern Lake Huron and Georgian Bay. Transactions of the American Fisheries Society, vol. 86, for the year 1956, pp. 128–134.

Buettner, Howard J.
1961. Recoveries of tagged, hatchery-reared lake trout from Lake Superior. Transactions of the American Fisheries Society, vol. 90, No. 4, pp. 404–412.

Carbine, William F., and Vernon C. Applegate.
1948. The movement and growth of marked northern pike (*Esox lucius* L.) in Houghton Lake and the Muskegon River. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 32, for the year 1946, pp. 215–238.

Dryer, William R.
1963. Age and growth of the whitefish in Lake Superior. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 63, No. 1, pp. 77–95.

Eschmeyer, Paul H.
1959. Survival and retention of tags, and growth of tagged lake trout in a rearing pond. U.S. Fish and Wildlife Service, Progressive Fish-Culturist, vol. 21, No. 1, pp. 17–21.

Eschmeyer, Paul H., and Walter R. Crowe.
1955. The movement and recovery of tagged walleyes in Michigan, 1929–1953. Michigan Department of Conservation, Institute for Fisheries Research, Miscellaneous Publication No. 8, pp. 1–32.

Eschmeyer, Paul H., Russell Daly, and Leo F. Erkkila.
1953. The movement of tagged lake trout in Lake Superior, 1950–1952. Transactions of the American Fisheries Society, vol. 82, for the year 1952, pp. 68–77.

Eschmeyer, R. W., and Alden M. Jones.
1941. The growth of game fishes in Norris Reservoir during the first five years of impoundment. Transactions of the Sixth North American Wildlife Conference, pp. 222–240.

Markus, Henry C.
1933. The effects of tags upon fresh water fishes Transactions of the American Fisheries Society vol. 63, pp. 319–325.

Parker, Phillip S., and Robert E. Lennon.
1956. Biology of the sea lamprey in its parasiti phase. U.S. Fish and Wildlife Service, Research Report 44, pp. 1–32.

Shetter, David S.
1936a. The jaw-tag method of marking fish. Paper of the Michigan Academy of Science, Arts, and Letters, vol. 21, for the year 1935, pp. 651–653.
1936b. Shrinkage of trout at death and on preservation. Copeia, 1936, No. 1, pp. 60–61.

Smith, Lloyd L., Laurits W. Krefting, and Robert L. Butler.
1952. Movements of marked walleyes, *Stizostedion vitreum vitreum* (Mitchill), in the fishery of the Red Lakes, Minnesota. Transactions of the American Fisheries Society, vol. 81, for the year 1951, pp. 179–196.

Smith, Oliver H., and John Van Oosten.
1940. Tagging experiments with lake trout, white fish, and other species of fish from Lake Michigan Transactions of the American Fisheries Society vol. 69, for the year 1939, pp. 63–84.

Snyder, J. P.
1932. Tagged smallmouth black bass in Lake Ontario, New York. Transactions of the American Fisheries Society, vol. 62, pp. 380–381.

Wilson, Robert C.
1953. Tuna marking, a progress report. California Fish and Game, vol. 39, No. 4, pp. 429–442.

AGE, GROWTH, SEX RATIO, AND MATURITY OF THE WHITEFISH IN CENTRAL GREEN BAY AND ADJACENT WATERS OF LAKE MICHIGAN

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ABSTRACT

This study is based on 1,023 whitefish, *Coregonus clupeaformis* (Mitchill)—819 in seven samples from five localities in central Green Bay in 1948–49 and 1951–52 and 204 in a single 1948 collection from northwestern Lake Michigan proper.

Records of age indicated unusual strength for only one year class—1943 which strongly dominated the 1948 sample from Lake Michigan and the 1949 sample from Green Bay and was well represented in the 1948 collection from Green Bay. Collections of 1951–52 without exception were dominated by age group III.

Length distributions of samples varied widely according to the age composition. Among fish more than 2 years old, the length distributions of age groups overlapped broadly. Several 1-inch intervals included fish of four age groups.

The length-weight relation varied considerably among central Green Bay samples, but differences among localities were nearly equalled by the year-to-year difference at a single locality. Lake Michigan whitefish were generally lighter than those from Green Bay. Weight increased to the 3.386 power of length in Green Bay (combined samples) and the 3.359 power in Lake Michigan.

Growth in length, calculated by direct proportion from diameter measurements of growth fields on scales, differed among localities in central Green Bay and between samples of different years at a single locality. If permanent locality differences exist they are not large and can be obscured by the evident annual fluctuations of growth. The grand average calculated length of Green Bay whitefish (combined collections) exceeded that of Lake Michigan fish in all years of life. The advantage was greatest (2.2 inches) at 3 years (calculated lengths of 16.0 and 13.8 inches) and subsequently declined to 0.5 inch at 9 years (lengths of 24.6 and 24.1 inches). Both groups reached the minimum legal length of 17 inches during the fourth growing season. Green Bay whitefish also had the larger calculated weights. The advantage reached 9.3 ounces in 3 years (calculated weights of 22.4 and 13.1 ounces). In years of life 4–9, the weight advantage over Lake Michigan fish ranged from 8.7 ounces, (seventh year; weights of 74.4 and 65.7 ounces) to 12.2 ounces (ninth year; weights of 96.2 and 84.0 ounces).

Comparison of growth of whitefish at four localities in northern Lake Michigan indicates that fastest growth is in central Green Bay and slowest near the Fox Islands. Growth is intermediate and similar in northwestern Lake Michigan proper and northern Green Bay.

Youngest mature male whitefish in Green Bay belonged to age group II and youngest mature females to age group III. All IV-group fish were mature. Shortest mature males were at 14.5–14.9 inches and shortest mature females at 16.5–16.9 inches. All males longer than 17.9 inches and all females longer than 18.4 inches were mature.

The whitefish, *Coregonus clupeaformis* (Mitchill), long has been a major commercial species in the Great Lakes. It occurs in all five lakes. Publications on Great Lakes whitefish include: Hart (1931), Lake Ontario; Van Oosten and Hile (1949), Lake Erie; Van Oosten (1939), Lake Huron; Roelofs (1958), Lake Michigan; and the most recent studies in Lake Superior by Edsall (1960) and Dryer (1963).

Some of these studies revealed the existence of populations with greatly different growth characteristics within the same lake and separated by

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only relatively short distances. The present paper discloses a similar situation between central Green Bay waters of Lake Michigan and the adjacent area of the lake proper. The knowledge of the existence and location of the various separate populations of whitefish is valuable to the sound management and commercial exploitation of the species.

MATERIALS AND METHODS

This study is based on 1,023 whitefish collected in six areas of central Green Bay and adjacent waters of Lake Michigan from 1948 through 1952 (fig. 1; table 1). The numbers of fish in individual samples ranged from 204 from the Europe Bay area of Lake Michigan to 80 at Peshtigo. The 230 fish at Minneapolis Shoals (131 on July 31, 1952, and 99 on September 16, 1952) had such closely similar growth and size that they were treated as a single collection. All collections were complete catches from the nets.

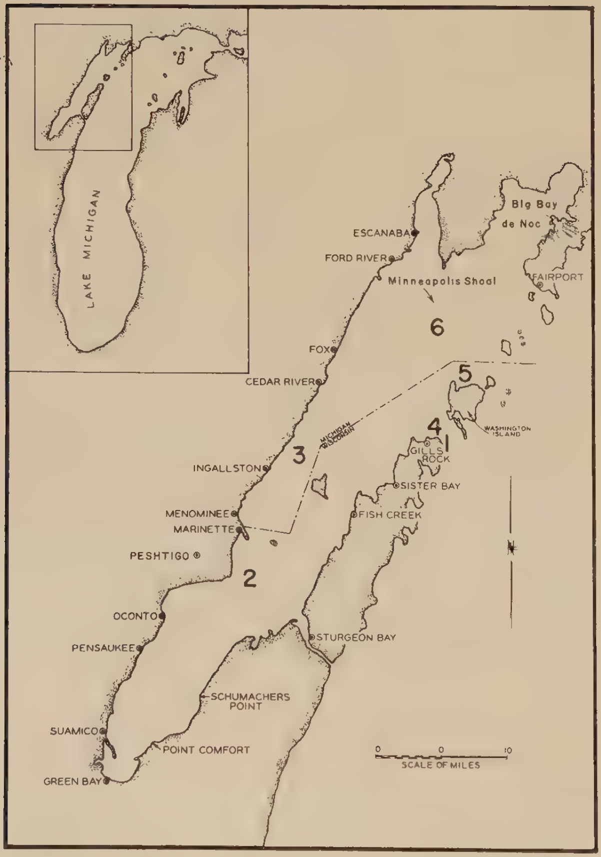


Figure 1.—Localities at which whitefish were collected in Lake Michigan proper and central Green Bay. The locality numbers are used in table 1 to identify individual samples.

Several other samples of selected fish, or samples too small to be used effectively for comparison with the larger collections, were employed in the section on the length-weight relation.

Table 1.—*Locality, gear, and date of capture of whitefish from Lake Michigan and central Green Bay*

[Figures in parentheses are used to identify localities in figure 1]

Date of capture	Locality	Gear	Number of fish
1948			
Oct. 14	Lake Michigan (1)	4½-inch-mesh pound net	20
Oct. 13	Peshtigo (2)	4¾- to 5-inch mesh gill net	8
1949			
May 18	Cedar River (3)	5-inch-mesh pound net	18
1951			
June 15	Cedar River (3)	4½-inch-mesh pound net	8
June 11	Gills Rock (4)	4½-inch-mesh pound net	12
1952			
Feb. 14	Washington Island (5)	4½-inch-mesh gill net	11
July 31	Minneapolis Shoals (6).	5-inch-mesh pound net	13
Sept. 16	Minneapolis Shoals (6).	5-inch-mesh pound net	9

All available data have been applied to each matter under consideration. As a result, certain discrepancies appear in numbers of fish. For example, a table giving the length-frequency distribution or the length-weight relation for an entire sample may be based on more fish than a table of age composition for the same sample. The latter table, of necessity, excludes those fish for which scales could not be read.

Scales were removed from the left side of the fish between the lateral line and the middle of the base of the dorsal fin. Total lengths (tip of the head to the tip of the tail, lobes compressed) were measured to the nearest 0.1 inch. Weights were determined with spring balances and recorded to the nearest quarter or half ounce. All records were later converted to the nearest 0.1 ounce. The sex was determined for all fish but maturity data were lacking or incomplete for all but the Minneapolis Shoals collections.

Scale impressions were made in cellulose acetate (Smith, 1954) and examined by means of a microprojector at a magnification × 44 (Moffett, 1952). Diameters of scales and of growth fields within were measured to the nearest 0.1 inch along a line through the focus that approximately bisected the anterior field.

Since the data in this study were not adequate for a precise determination of the body-scale relation all calculations of length were by direct proportion. A plot of the available data did indicate a straight line with an intercept value near zero. This observation disagrees with that of Edsall (1960) who found the relation for Munising Bay (Lake Superior) whitefish to be linear with an intercept of 1.486 inches on the axis of fish length. It agrees, however, with the finding of Van Oosten (1923) for whitefish reared in the New York Aquarium and of Dryer (1963) for Lake Superior whitefish from the Apostle Islands region.

All fish were considered to become a year older on January 1; an annulus was credited at the edge of the scale from that date until the current-season annulus was completed. Age groups are designated by Roman numerals corresponding to the number of annuli.

None of the fish collected in spring or early summer had started growth. At Minneapolis Shoals, growth was in progress in July and September but no difficulty was encountered in locating the outermost annulus.

Growth of the Lake Michigan and Peshtigo samples collected in mid-October 1948 has been assumed to be complete for the year. The lengths at capture of age groups in these samples as well as in samples taken in the spring or early summer are therefore treated also as calculated lengths.

On the basis of findings detailed in later text sections it was determined desirable to treat the sample from the Europe Bay area of Lake Michigan separately from the central Green Bay collections; fish from Europe Bay have been designated "Lake Michigan." The collections made within Green Bay are identified by actual locality of capture or labeled collectively as "Central Green Bay."

In the presentation of data, the collections are arranged in the order of capture with two exceptions. The Lake Michigan collection always appears first despite its collection a day later than the one from Peshtigo because the fish are distinct from the central Green Bay fish; again in 1951 the Cedar River sample is placed in tables in advance of the Gills Rock collection to take advantage of ready comparisons of the Cedar River collections of 1949 and 1951—the only two collections from the same locality.

AGE COMPOSITION

The records of age composition point clearly to the presence of only one exceptionally strong year class of whitefish—that of 1943 (table 2; fig. 2). It was strongly dominant as the V group in the Lake Michigan sample in 1948 (52.7 percent) and as the VI group at Cedar River (65.2 percent) in 1949. It was also abundant (38.7 percent) at Peshtigo in 1948 although outnumbered by the IV group (49.4 percent). It had disappeared, however, by 1951.

The collections of 1951 and 1952 from Cedar River, Gills Rock, Washington Island, and Minneapolis Shoals were all dominated by age group III (fig. 2). Roelof's (1958) data showed that age group III provided 85 to 90 percent of the annual commercial catch in Big Bay de Noc waters of Lake Michigan in 1951–54. The author believed that mortality was extremely high from age group III to age group IV.

The use of two types of gear (gill and pound nets) to catch fish made it possible to study their effect on age composition in the samples. The gill net is designed to catch fish above a certain size but does not catch the largest fish. The pound net is not so selective, as the effect of its leaders and the mechanical action of lifting the net frequently result in the capture of small fish. Although many more of these smaller fish escape than are actually caught, some do mill around and avoid escape through the larger side meshes until they are trapped during lifting and are retained. It was this fishing action that permitted the capture of six I-group fish by pound nets; no fish of that age appeared in gill net samples. The pound net also can take the larger fish which cannot be caught readily in a gill net.

The Washington Island gill net sample showed that these various gear effects did not alter the basic composition of dominance by III-age fish during 1951–52. The Peshtigo sample did have fewer V-group fish than would be expected on the basis of the strong dominance of the 1943 year class in the Lake Michigan collection of 1948 and the Cedar River collection of 1949. The Peshtigo sample was small (only 80 fish), however,

TABLE 2.—*Age and year-class composition of samples of whitefish from Lake Michigan and central Green Bay*

Locality, year of capture, and item	Year class												Avera or tot
	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	
Lake Michigan, 1948:													
Age group	VIII	---	VI	V	IV	III	II	I	---	---	---	---	
Number	1	---	3	106	20	27	40	4	---	---	---	---	
Percentage	0.5	---	1.5	52.7	10.0	13.3	20.0	2.0	---	---	---	---	---
Peshtigo, 1948:													
Age group	---	---	---	V	IV	III	---	---	---	---	---	---	
Number	---	---	---	29	37	9	---	---	---	---	---	---	
Percentage	---	---	---	38.7	49.4	11.9	---	---	---	---	---	---	---
Cedar River, 1949:													
Age group	IX	VIII	VII	VI	V	IV	III	II	---	---	---	---	
Number	2	2	2	114	3	15	34	3	---	---	---	---	
Percentage	1.1	1.1	1.1	65.2	1.7	8.6	19.5	1.7	---	---	---	---	---
Cedar River, 1951:													
Age group	---	---	---	---	---	V	IV	III	---	---	---	---	
Number	---	---	---	---	---	I	7	70	---	---	---	---	
Percentage	---	---	---	---	---	1.3	8.9	89.8	---	---	---	---	---
Gills Rock, 1951:													
Age group	---	---	---	---	---	---	IV	III	II	I	---	---	
Number	---	---	---	---	---	---	5	78	41	1	---	---	
Percentage	---	---	---	---	---	---	4.0	62.4	32.8	0.8	---	---	---
Washington Island, 1952:													
Age group	---	---	---	---	---	---	---	---	IV	III	---	---	
Number	---	---	---	---	---	---	---	---	21	89	---	---	
Percentage	---	---	---	---	---	---	---	---	19.1	80.9	---	---	---
Minneapolis Shoals, 1952:													
Age group	---	---	---	---	---	---	---	---	IV	III	II	I	
Number	---	---	---	---	---	---	---	---	5	162	59	1	
Percentage	---	---	---	---	---	---	---	---	2.2	71.4	26.0	0.4	---

[1] The first of each pair of figures is the average number of annuli.

and may not have been fully representative of the local stock.

The average number of annuli in the 1948–49 samples ranged from 4.0 to 5.2 as compared to 2.7 to 3.2 in the 1951–52 samples (table 2). This difference in average age is traceable to the great strength of the 1943 year class at ages V and VI.

The 1943 year class of whitefish was abundant in Lake Huron as well as in Lake Michigan. Saginaw Bay of Lake Huron, for example, showed an average commercial production of 26,000 pounds during 1938–45, an increase to an average of 807,000 pounds during 1946–48, and a decline to an average of 17,000 pounds during 1949–56 (Hile and Buettner, 1959).

The effect of the 1943 year class of whitefish on the commercial production from the Wisconsin waters of Lake Michigan and the Michigan waters of Lakes Michigan and Huron is shown by the records of catch for 1940–51 (table 3—data from Baldwin and Saalfeld, 1962).

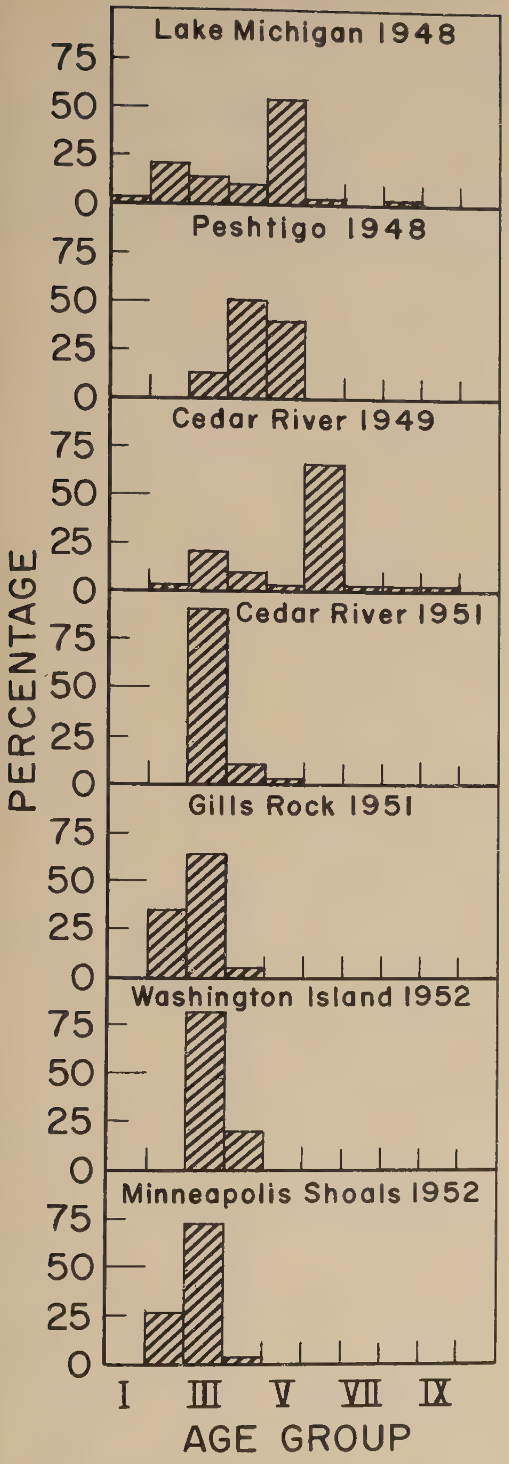
Production in all three areas showed a marked increase in 1946, reached peaks in 1947 or 1948 and thereafter declined to the level of the early 1940's. A feature of the record is the longer period of high catch in Michigan waters of Lake Michigan than in the other two waters; the bulk of this production came from Green Bay.

The same year also saw a strong year class another coregonine, the lake herring, *Coregon artedi*, in Green Bay. Following low productio over the period 1939–44 (high of 697,000 pound in 1939 and a low of 285,000 pounds in 1942) th commercial take of lake herring in State Michigan waters of Green Bay rose to 2,668,00 pounds in 1948 (Hile, Lunger, and Buettne 1953).

TABLE 3.—*Production (thousands of pounds) of whitefish Wisconsin and Michigan waters of Lake Michigan ar Michigan waters of Lake Huron, 1940–51*

Year	Lake Michigan		Lake Huro Michigan
	Wisconsin	Michigan	
1940	197	754	1
1941	401	896	1
1942	279	1,061	
1943	254	1,152	1
1944	343	1,403	1
1945	331	1,326	1
1946	735	1,822	5
1947	1,807	4,018	3,0
1948	985	4,263	2,9
1949	485	3,007	5
1950	259	2,102	1
1951	242	971	1

Coregonines were not alone in the production strong 1943 year classes in Lakes Michigan an Huron, as the commercial production of walley *Stizostedion vitreum*, likewise rose impressivel This increase was most dramatic in State Michigan waters of Green Bay, where it rose fro



IGURE 2.—Age composition of whitefish from Lake Michigan and central Green Bay.

e 1929–43 mean of 51,000 pounds to 1,063,000 ounds in 1949 (Hile, Lunger, and Buettner, 953). Hile (1950) showed that 93.6 percent of a sample of 109 fish taken in the spring of 1949 were 6 years old, and Pycha (1961) gave a complete history of the 1943 year class.

The walleye production in Saginaw Bay, Lake Huron, experienced a rapid decline from an all-time high commercial production of over 2 million pounds in 1942. This decrease was interrupted, however, by a temporary rise in 1946. Hile and Buettner (1959) stated "The recovery of walleyes in 1946 can be attributed to the great strength of the 1943 year class (unpublished records of age)."

LENGTH DISTRIBUTION

No single sample of whitefish in this study is truly suitable for demonstrating a "typical" distribution of the catch of commercial gear. As is common among the coregonines, one age group strongly dominated each sample (see previous section on age composition). This dominance caused individual samples to have a relatively tight length distribution with high modes.

The range of length, mean length, position and relative height of mode, and the percentage of legal-size whitefish varied greatly from collection to collection (table 4), but the seven samples fell clearly into two generally similar groups—the three samples of 1948–49 and the four of 1951–52.

The 1948–49 samples showed high mean lengths (18.9–20.1 inches), high modal lengths (19–21 inches), and high percentages of legal fish (68–96). Dominance or great abundance of the 1943 year class at a time its members had completed 6 growing seasons caused these high values.

The 1951–52 samples were all dominated by III-group fish; consequently the mean lengths (15.6–17.5 inches), the modal lengths (16 or 17 inches), and the percentages of legal fish (41–67) were all lower than in the other group.

The records of table 4 give evidence that pound nets capture more smaller whitefish than do gill nets. Neither of the gill net samples (Peshtigo and Washington Island) included fish shorter than 15.0 inches, whereas four of five pound net samples included smaller fish—some in considerable numbers. Particularly striking is the contrast between the Peshtigo and Lake Michigan samples which were collected on consecutive days.

The individual collections were poorly suited also to show the length distribution of age groups. A single collection usually yielded dependable data on the length distribution of only one age group.

Table 4.—*Distribution of total length of whitefish from Lake Michigan and central Green Bay*

[Includes a small number of fish for which ages could not be determined; asterisks indicate modes]

Length interval	Location and year of collection						
	Michigan (1948)	Peshtigo (1948)	Cedar River (1949)	Cedar River (1951)	Gills Rock (1951)	Washington Island (1952)	Minneapolis Shoals (1952)
Inches	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*
7.0–7.9					1		
8.0–8.9							
9.0–9.9	1						
10.0–10.9	2				4		
11.0–11.9	1				8		1
12.0–12.9	3		3		13		
13.0–13.9	17		1		14		4
14.0–14.9	17		3		2		25
15.0–15.9	12	1	13	2	5	9	30
16.0–16.9	12	2	16	26	29	*55	35
17.0–17.9	5	9	8	*43	*45	28	*96
18.0–18.9	7	16	10	7	5	10	34
19.0–19.9	8	*20	6	4	2	5	3
20.0–20.9	*52	19	25	1	1	5	2
21.0–21.9	47	13	*58				
22.0–22.9	14		25			1	
23.0–23.9	5		9	1			
24.0–24.9			5	1			
25.0–25.9							
26.0–26.9	1						
Number of fish	204	80	182	85	129	113	230
Percentage at mode	25.5	25.0	31.9	50.6	34.9	48.7	41.7
Average length	18.9	19.4	20.1	17.5	15.6	17.2	16.8
Percentage legal [1]	68.2	96.2	80.2	67.0	41.1	43.4	58.6

[1] Total length, 17 inches or longer; actually, the size limit in State of Michigan waters was not changed from 2 pounds (round) to 17 inches until 1953.

The pooling of length data for fish of corresponding age in different samples, because of annual differences and possible local differences in growth, extends the range somewhat beyond that which would be expected in a single sample of fish of that age and broadens the modal region but does provide a useful idea of the general range and distribution.

Records obtained by the pooling of collections from central Green Bay (table 5) yielded fairly good information on the length distribution of whitefish that had completed 2–6 growing seasons and some data on lengths at other ages. In order to describe the distribution of total lengths in terms of completed growing seasons of the whitefish from central Green Bay, the Minneapolis Shoals collection was not included. Omission of this group, the only one in which growth was in progress when the samples were collected, made it possible to give lengths in terms of completed seasons without the use of any calculated lengths.

If length intervals with only one fish are excluded, length ranges of fish that had completed 2–6 seasons of growth were 5 inches for all but the 6-season fish, which had a range of 6 inches. When all fish are considered, the greatest range was 9 inches (15.0–23.9 inches) for fish that had completed 5 growing seasons. Overlap of lengths for growing seasons 3 through 6 was substantial. Fish 17.0–19.9 inches long could have completed 3, 4, 5, or 6 growing seasons. Every 1-inch length interval above 14 inches included fish of at least 2 ages and usually 3 or 4.

Table 5.—*Distribution of total length of whitefish from central Green Bay that had completed one to nine growing seasons*

[Asterisks indicate modes; the lower half of the broad mode at two growing seasons is the one nearer the mean]

Length interval	Completed growing seasons								
	1	2	3	4	5	6	7	8	9
Inches	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*
7.0–7.9	1								
8.0–8.9									
9.0–9.9									
10.0–10.9		4							
11.0–11.9		8							
12.0–12.9		*15							
13.0–13.9		15							
14.0–14.9		2	2						
15.0–15.9			28		1				
16.0–16.9			*120	3	1				
17.0–17.9			109	13	4	1			
18.0–18.9			11	*23	11	2			
19.0–19.9			1	11	*15	5			
20.0–20.9				6	4	37			
21.0–21.9					4	*65			
22.0–22.9				1		24	1		
23.0–23.9					1	9			
24.0–24.9							1	2	
Number of fish	1	44	271	57	41	143	2	2	
Average length	7.1	12.4	16.7	18.5	19.2	21.2	23.8	24.6	24.
Percentage legal [1]	.0	.0	44.7	94.7	95.2	100.0	100.0	100.0	100.

[1] Total length, 17 inches or longer; actually, the size limit in State of Michigan waters was not changed from 2 pounds (round) to 17 inches until 1953.

LENGTH-WEIGHT RELATION

Whitefish from central Green Bay exhibited considerable sample-to-sample differences in the length-weight relation but the data gave no reason for a conclusion that stocks with different length-weight relations exist in the area (table 6). The Cedar River samples of 1949 and 1951 (both collected in late spring) showed an annual difference as great or nearly as great (3.9 ounces at 17.2 inches; 3.7 ounces at 18.2 inches; and 7.3 ounces at 18.7 inches) as is found between samples from different locations (2.9 ounces at 17.2 inches between Gills Rock and Washington Island; 5.8 ounces at 18.2 and 18.7 inches between Washington Island and Minneapolis Shoals). The pooling of all the central Green Bay samples therefore gives the most useful length-weight information.

The annual weight differences as demonstrated by the Cedar River samples are comparable to fluctuations described for other coregonines (Deason and Hile, 1947, for the kiyi, *Coregonus kiyi*; Van Oosten and Hile, 1949, for the Lake Erie whitefish; Morawa, 1960, whose data showed that adult *Coregonus fera* in Lake Geneva, Switzerland, could lose 25 percent of their weight and 63 percent of their fat between summer and the fall spawning season).

TABLE 6.—*Length-weight relation of whitefish from Lake Michigan and central Green Bay collections*

Total length [1]	Location and year of collection						
	Michigan (1948)	Peshtigo (1948)	Cedar River (1949)	Cedar River (1951)	Gills Rock (1951)	Washington Island (1952)	Minneapolis Shoals (1952)
Inches	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
.2					1.6		
.7							
.2							
.7							
.2							
.7	4.0						
0.2	4.0				5.6		
0.7	6.5				6.0		
1.2					7.0		6.5
1.7	8.0				8.2		
2.2	8.5		9.3		9.3		
2.7	9.1				10.6		
3.2	11.6		12.0		12.2		
3.7	12.9				13.5		12.8
4.2	15.2				17.0		14.2
4.7	15.8		18.0		18.0		16.5
5.2	18.0		20.8			25.0	18.2
5.7	19.7	25.0	22.3	22.5	20.3	24.0	20.4
6.2	22.1		25.2	22.7	23.9	26.3	23.0
6.7	26.0	26.5	27.2	24.3	26.8	29.7	24.6
7.2	26.0	34.5	30.7	26.8	29.1	32.0	27.0
7.7	33.4	36.5	34.5	29.9	28.6	32.8	29.8
8.2	32.7	38.8	34.4	30.7	35.7	38.0	32.2
8.7	37.5	43.5	40.8	33.5	42.5	40.5	34.7
9.2	38.8	43.4	38.8	39.5	40.0	40.1	
9.7	42.0	48.0	46.4	42.7	49.0		43.7
0.2	47.7	53.7	48.8	47.5	52.0	48.7	49.0
0.7	52.7	53.6	54.2			53.0	54.0
1.2	56.3	59.1	56.4				
1.7	61.2	65.2	61.5				
2.2	67.7		64.6			70.5	
2.7	65.3		69.6				
3.2	73.8		77.2				
3.7	85.9		79.2	79.5			
4.2			78.0				
4.7			93.1				
5.2							
5.7							
6.2	100.0						

[1] Midpoints of 0.5-inch intervals.

The Lake Michigan sample of 1948 is held to be different from the central Green Bay fish on the basis of mean weights much lighter than those of the Peshtigo fish collected only a day earlier (26.0 and 34.5 ounces at 17.2 inches; 32.7 and 38.8 unces at 18.2 inches; 38.8 and 43.4 ounces at 9.2 inches); the Lake Michigan fish furthermore were generally lighter than those of other Green Bay samples (table 6).

A length-weight equation, to be most useful, should include fish of both sexes, sampled at various times of the year over a period of years. Bias from annual and seasonal variations, sex differences, and maturity and state of sex organs is minimized by this procedure. The resulting general curve, though not exactly descriptive of fish collected at any given time and considerably different from those of some samples, produces the most usable record.

The samples from central Green Bay meet the above-stated requirements fairly well because both sexes are represented and collection dates covered all seasons—the Peshtigo sample in mid-October 1948; the Cedar River samples in May 1949 and June 1951, the Gills Rock sample in June 1951, the Washington Island sample in February 1952, and the Minneapolis Shoals sample in July and September 1952. Selected fish taken at other times were also used to provide more small individuals. Effects of annual and seasonal fluctuations on determination of the length-weight relation were therefore lessened to a fair degree in central Green Bay. The Lake Michigan data, on the other hand, are based on a single October sample.

Length-weight equations were derived for the Lake Michigan sample and the central Green Bay samples by fitting straight lines by least squares to the logarithms of the lengths and weights. The curves in figure 3 are the graphs of the following equations:

Lake Michigan

$$W=1.9422\times10^{-3}\,L,^{3.35903}$$

Central Green Bay

$$W=1.8756\times10^{-3}\,L,^{3.38647}$$

where

W=weight in ounces,

and

L=total length in inches.

The weight of the Lake Michigan whitefish increased as the 3.35903 power of the length, and the weight of the central Green Bay fish as the 3.38647 power of the length. The difference between the exponents cannot be considered great. Both equations show a substantial departure from the cube relation; plumpness increasesco nsiderably with increase of length.

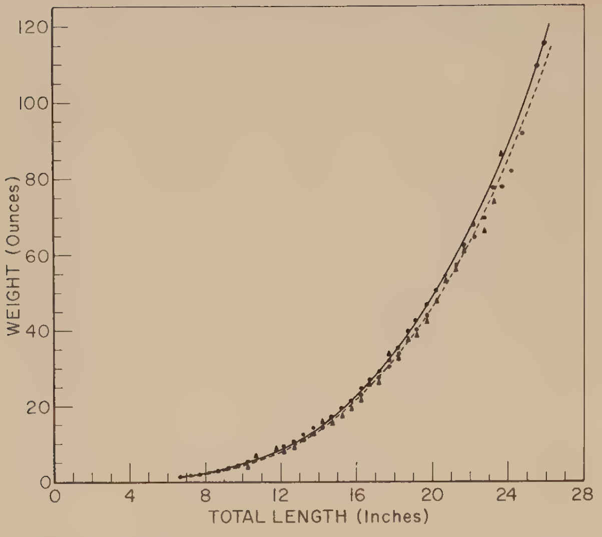


FIGURE 3.—Length-weight relation of whitefish from Lake Michigan and central Green Bay. The broken line represents the calculated weights and the triangles the empirical weights of the Lake Michigan fish; the solid line and dots represent the central Green Bay fish.

Agreement of empirical and calculated weights of the Lake Michigan whitefish (table 7; fig. 3) varied considerably according to length and number of fish. Over the length range, 20.2–22.2 inches, where the fish were most plentiful, the empirical weights were all higher than the calculated weights by 0.6–3.1 ounces. The length range, 9.7–19.7 inches, had empirical weights both greater and smaller than the calculated weights. The maximum deviation of empirical weight below the calculated was 1.4 ounces at 17.2 inches, and the maximum deviation above the calculated weight was 3.1 ounces at the next interval, 17.7 inches. At 11 lengths the empirical weight was less than the calculated, and at 8 it was greater. The greatest disagreement over the entire length range was 12.8 ounces at 26.2 inches (only one fish).

The empirical weights of the Green Bay fish were below the calculated weights at lengths above 21.2 inches; the discrepancies ranged from a low of 1.0 ounce at 21.7 inches to a high of 9.5 ounces at 24.2 inches. Over the remainder of the length range (6.7–20.7 inches) empirical and calculated weights were the same at 4 lengths, differed by only 0.1 or 0.2 ounce at 14 and disagreed by 0.5–1.8 ounces at 10. At 16 of the 24 lengths where the two weights differed, the empirical weight was less than the calculated weight.

TABLE 7.—*Length-weight relation of whitefish from Lak Michigan and in the combined collections from central Gree Bay*

[Calculated weights from equations given in text]

Total length [1]	Lake Michigan			Central Green Bay		
	Number of fish	Weight		Number of fish	Weight	
		Calculated	Empirical		Calculated	Empi ical
Inches		*Ounces*	*Ounces*		*Ounces*	*Ounce*
6.7		1.1		6	1.1	1.
7.2		1.4		15	1.6	1.
7.7		1.9		27	1.9	2.
8.2		2.2		26	2.3	2.
8.7		2.8		12	2.8	2.
9.2		3.3		5	3.5	3.
9.7	1	4.0	4.0		4.2	
10.2	1	4.8	4.0	8	4.9	5.
10.7	1	5.5	6.5	10	5.8	5.
11.2		6.4		11	6.7	6.
11.7	1	7.6	8.0	19	7.7	7.
12.2	1	8.6	8.5	15	8.9	9.
12.7	2	9.9	9.1	12	10.3	10.
13.2	6	11.3	11.6	13	11.6	12.
13.7	11	12.8	12.9	9	13.3	13.
14.2	7	14.5	15.2	17	14.9	14.
14.7	10	16.1	15.8	16	16.9	17.
15.2	7	18.2	18.0	33	18.8	19.
15.7	5	20.2	19.7	42	21.1	21.
16.2	6	22.5	22.1	81	23.4	24.
16.7	6	24.9	26.0	89	25.9	26.
17.2	3	27.4	26.0	133	28.7	28.
17.7	2	30.3	33.4	89	31.6	30.
18.2	3	33.3	32.7	56	34.7	33.
18.7	4	36.4	37.5	27	38.0	39.
19.2	4	39.7	38.8	22	41.6	41.
19.7	4	43.3	42.0	14	45.4	46.
20.2	23	47.1	47.7	20	49.3	50.
20.7	29	51.2	52.7	29	53.7	53.
21.2	25	55.4	56.3	39	58.2	57.
21.7	22	59.9	61.2	32	62.9	61.
22.2	11	64.6	67.7	17	68.0	64.
22.7	3	69.7	65.3	12	73.3	69.
23.2	3	74.9	73.8	5	78.9	77.
23.7	2	80.6	85.9	10	84.9	77.
24.2		86.5		2	91.0	81.
24.7		92.6		5	97.6	91.
25.2		99.0			104.5	
25.7		105.7			111.6	
26.2	1	112.8	100.0		119.1	

[1] Midpoint of 0.5-inch intervals.

CALCULATED GROWTH IN LENGTH

The records of sex for all fish made it possible to study sex difference in growth rate. No difference was found in four of the seven collections; females grew slightly faster in two and males in one. Because sex differences were nil or small, and did not favor either males or females, separation of the sexes was not justified. The growth of whitefish at each locality was described by combining the data for males and females. The mean calculated length at the end of each year of life was determined for each age group of the various samples (tables 8–14).

The calculated lengths of the whitefish in the various collections give little evidence of "Lee's phenomenon" of decrease of growth rate with increase in the age of the fish for which lengths are computed. Among the collections in which

TABLE 8.—*Calculated total length of whitefish taken from Europe Bay area of Lake Michigan, October 14, 1948*

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life								
		1	2	3	4	5	6	7	8	9
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
I	4	6.5	*10.5							
II	40	6.4	10.6	*14.1						
III	27	5.7	10.2	13.9	*16.5					
IV	20	5.9	9.7	14.7	18.0	*20.1				
V	106	5.1	9.5	13.4	17.0	19.4	*21.1			
VI	3	6.3	10.1	14.9	18.5	20.6	22.2	*23.2		
VIII	1	5.5	12.2	16.3	19.2	21.5	23.1	24.2	25.2	*26.0
Grand average calculated length		5.6	9.8	13.8	17.1	19.5	21.2	23.4	25.2	26.0
Increment of average		5.6	4.2	4.0	3.3	2.4	1.7	2.2	1.8	0.8
Grand average increment of length		5.6	4.2	4.0	3.4	2.4	1.6	1.1	1.0	0.8
Sum of average increments		5.6	9.8	13.8	17.2	19.6	21.2	22.3	23.3	24.1

TABLE 9.—*Calculated total length of whitefish taken at Peshtigo, October 13, 1948*

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life					
		1	2	3	4	5	6
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
III	9	5.8	11.5	15.6	*18.0		
IV	37	6.1	10.8	14.8	17.6	*19.0	
V	29	6.4	11.7	15.2	17.7	19.3	*20.5
Grand average calculated length		6.2	11.2	15.0	17.7	19.1	20.5
Increment of average		6.2	5.0	3.8	2.7	1.4	1.4
Grand average increment of length		6.2	5.0	3.8	2.7	1.5	1.2
Sum of average increments		6.2	11.2	15.0	17.7	19.2	20.4

TABLE 10.—*Calculated total length of whitefish taken at Cedar River, May 18, 1949*

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life								
		1	2	3	4	5	6	7	8	9
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	2	7.0	*12.6							
III	34	6.5	11.6	*16.1						
IV	15	5.9	10.7	15.3	*18.3					
V	3	5.9	10.7	15.3	17.9	*19.1				
VI	114	5.8	11.0	15.1	18.3	20.2	*21.6			
VII	2	8.3	12.9	17.5	20.1	21.7	22.8	*23.8		
VIII	2	7.8	13.8	17.4	20.3	21.6	22.7	23.1	*24.5	
IX	2	7.7	10.5	15.9	18.9	20.6	21.9	23.1	23.8	*24.5
Grand average calculated length		6.0	11.1	15.4	18.3	20.3	21.7	23.3	24.1	24.5
Increment of average		6.0	5.1	4.3	2.9	2.0	1.4	1.6	0.8	0.4
Grand average increment of length		6.0	5.1	4.3	3.2	1.9	1.4	0.9	1.0	0.7
Sum of average increments		6.0	11.1	15.4	18.6	20.5	21.9	22.8	23.8	24.5

TABLE 11.—*Calculated total length of whitefish taken at Cedar River, June 15, 1951*

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life				
		1	2	3	4	5
		Inches	*Inches*	*Inches*	*Inches*	*Inches*
III	70	6.8	12.3	*17.1		
IV	7	5.9	10.7	15.4	*18.5	
V	1	7.5	13.4	17.3	21.2	*23.6
Grand average, calculated length		6.8	12.1	16.9	18.8	23.6
Increment of average		6.8	5.3	4.8	1.9	4.8
Grand average increment of length		6.8	5.3	4.8	3.2	2.4
Sum of average increments		6.8	12.1	16.9	20.1	22.5

TABLE 12.—*Calculated total length of whitefish taken at Gills Rock, June 11, 1951*

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life			
		1	2	3	4
		Inches	*Inches*	*Inches*	*Inches*
I	1	*7.1			
II	41	7.1	*12.4		
III	78	6.9	12.3	*16.9	
IV	5	7.4	10.9	14.8	*18.2
Grand average calculated length		7.0	12.2	16.7	18.2
Increment of average		7.0	5.2	4.5	1.5
Grand average increment of length		7.0	5.2	4.5	3.4
Sum of average increments		7.0	12.2	16.7	20.1

TABLE 13.—*Calculated total length of whitefish taken north of Washington Island, February 14, 1952*

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life			
		1	2	3	4
		Inches	*Inches*	*Inches*	*Inches*
III	89	7.4	12.5	*16.6	
IV	21	6.5	12.0	16.2	*19.1
Grand average calculated length		7.3	12.4	16.6	19.1
Increment of average		7.3	5.1	4.2	2.5
Grand average increment of length		7.3	5.1	4.2	2.9
Sum of average increments		7.3	12.4	16.6	19.5

TABLE 14.—*Calculated total length of Whitefish taken at Minneapolis Shoals, July 31 and September 16, 1952*

Age group	Number of fish	Length at capture	Calculated length at end of year of life			
			1	2	3	4
		Inches	*Inches*	*Inches*	*Inches*	*Inches*
I	1	11.2	7.5			
II	59	15.0	7.0	12.1		
III	162	17.4	6.9	11.6	15.5	
IV	5	20.1	6.0	12.2	16.0	18.8
Grand average calculated length			7.0	11.8	15.5	18.8
Increment of average			7.0	4.8	3.7	3.3
Grand average increment of length			7.0	4.8	3.8	2.8
Sum of average increments			7.0	11.8	15.6	18.4

few age groups were well represented (Peshtigo, 1948, and the three 1950–51 samples) the discrepancies in calculated length appear to be randomly distributed. The two samples that had fair to good representation of several age groups within the range II–VI (Lake Michigan, 1948; Cedar River, 1949) gave some indication of a progressive decline of calculated lengths with age of the younger fish and then an increase among the older fish.

The lack of a progressive change of growth with increase in age leads to closely similar results in the estimation of general growth by grand average calculated length and by the summation of grand average increments of length (see bottom portions of tables 8–14). The summation of increments does have the decided advantage, however, of smoothing out these irregularities brought about in the data for the later years of life by the successive dropping out of poorly represented age groups. Growth curves based on the annual increments were chosen, therefore, for the comparison of growth of whitefish in the different collections (table 15).

TABLE 15.—*Calculated total length of whitefish from Lake Michigan and central Green Bay*

[Based on successive addition of grand average increments]

Location and year of capture	Calculated length at end of year of life								
	1	2	3	4	5	6	7	8	9
1948	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*
Lake Michigan	5.6	9.8	13.8	17.2	19.6	21.2	22.3	23.3	24.
Peshtigo	6.2	11.2	15.0	17.7	19.2	20.4			
1949									
Cedar River	6.0	11.1	15.4	18.6	20.5	21.9	22.8	23.8	24.
1951									
Cedar River	6.8	12.1	16.9	20.1	22.5				
Gills Rock	7.0	12.2	16.7	20.1					
1952									
Washington Island	7.3	12.4	16.6	19.5					
Minneapolis Shoals	7.0	11.8	15.6	18.4					

The general growth data for the seven collections from six localities show considerable differences among calculated lengths for each year of life. The Lake Michigan whitefish stands clearly apart from all others, however, by reason of its poorer growth in the first 3 years of life. In all comparisons during the first 3 years of life the Lake Michigan fish are smaller; the minimum difference was 0.4 inch (1949 Cedar River fish at the end of the first year of life) and the maximum difference was 3.1 inches (1951 Cedar River fish at the end of the third year of life). Improved growth of the Lake Michigan fish in later years reduced the differences from the Green Bay fish to unimportance, but the form of the growth curve in the two areas was decidedly different. The growth of fish from Gills Rock, collected only a few miles from Europe Bay in Lake Michigan proper (fig. 1), differed from growth in Lake Michigan in about the same manner as did the growth of whitefish from other Green Bay localities.

The records for central Green Bay collections leave little doubt of the existence of real differences in the growth of whitefish of the various samples, but do not warrant any general conclusion on the presence of stocks with permanent and significant differences of growth. The substantial differences in growth (15.4 and 16.9 inches at the end of 3 years, and 18.6 and 20.1 inches at the end of 4 years) of fish in the two collections from Cedar River are much the same as the difference (15.0 and 16.6 inches at 3 years and 17.7 and 19.5 inches at 4 years) of fish from Peshtigo and Washington Island, or the difference (15.6 and 16.9 inches at 3 years and 18.4 and 20.1 inches at 4 years) of fish from Minneapolis Shoals and Cedar River, 1951.

Although the effects of such factors as random variability, gear selection, and segregation by size should not be discounted entirely, a major cause of variation in estimates of growth has been found by many investigators to be annual fluctuations of growth rate in combination with sample differences of year-class composition. The samples of the present study as a group are poorly suited for studies of fluctuations in growth—lack of collections in consecutive years from any locality, small numbers of well-represented age groups in the majority of samples. Two, however (Lake Michigan, 1948; Cedar River, 1949), do lend themselves to the type of analysis described by Hile (1941) and subsequently employed by numerous investigators.

Growth fluctuated from roughly 16 percent above to 13 percent below average (total range, 29 percent) in Lake Michigan and from 4 percent above to 3 percent below (total range, 7 percent) for Cedar River within the 6-year period 1943–48 (table 16). Fluctuations of this magnitude, especially those in Lake Michigan, can affect estimates of growth materially. Even wider year-to-year changes in growth of Lake Erie whitefish were reported by Van Oosten and Hile, 1947, who recorded a change from 15 percent above the 1924–30 average in 1927 to 25 percent below in 1930.

A feature of the data on fluctuations of growth is the close agreement between Lake Michigan and Cedar River collections. Without exception the direction of the annual change was the same in the two localities and the annual percentage deviations were also all on the same side of the mean. So close was the agreement that the coefficient of correlation (r) between the two series was 0.824, a value that is significant at the probability level $0.05 > p > 0.02$. Evidence is strong therefore that the factors that brought about changes in growth rate in the two areas were closely similar or had similar fluctuations.

If the differences among growth curves for the whitefish in the various samples from Green Bay were attributable primarily to fluctuations in growth rate, the calculated lengths of members of the same year class from different localities should agree very closely. The selected comparisons of table 17 do not lead to a clear conclusion. The three year classes collected at both Peshtigo and Cedar River (1943, 1944, and 1945) give evidence of a difference in the style of growth at the two localities. The calculated lengths for Peshtigo whitefish were greater than those of whitefish from Cedar River in 7 of 9 comparisons (exceptions 5.8 and 5.9 inches at the end of the first year for the 1945 year class; and 14.8 and 15.3 inches at 3 years for the 1944 year class) over the first 3 years of life, but the Peshtigo fish had the shorter calculated lengths in all of six comparisons beyond the third year.

TABLE 16.—*Annual fluctuations in the growth of whitefish in two samples expressed as percentage deviations from the 1943–48 mean*

[Estimates based on annual increments of length of age groups II–V of the 1948 collection from Lake Michigan and age groups III–VI of the 1949 collection from Cedar River; analysis followed procedure described by Hile (1941)]

Year	Percentage deviation from mean	
	Lake Michigan	Cedar River
1943	−7.8	−1.0
1944	6.7	.7
1945	−1.4	−3.0
1946	15.7	4.2
1947	.1	1.8
1948	−13.5	−2.6

TABLE 17.—*Comparisons of growth of whitefish of the same year class collected at different localities in central Green Bay*

[Data from tables 9–14]

Year class and locality	Year of capture	Age group	Number of fish	Calculated length at end of year of life					
				1	2	3	4	5	6
1943				*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
Peshtigo	1948	V	29	6.4	11.7	15.2	17.7	19.3	20.5
Cedar River	1949	VI	114	5.8	11.0	15.1	18.3	20.2	21.6
1944									
Peshtigo	1948	IV	37	6.1	10.8	14.8	17.6	19.0	------
Cedar River	1949	V	3	5.9	10.7	15.3	17.9	19.1	------
1945									
Peshtigo	1948	III	9	5.8	11.5	15.6	18.0	------	------
Cedar River	1949	IV	15	5.9	10.7	15.3	18.3	------	------
1948									
Cedar River	1951	III	70	6.8	12.3	17.1	------	------	------
Gills Rock	1951	III	78	6.9	12.3	16.9	------	------	------
Washington Island.	1952	IV	21	6.5	12.0	16.2	19.1	------	------
Minneapolis Shoals.	1952	IV	5	6.0	12.2	16.0	18.8	------	------
1949									
Gills Rock	1951	II	41	7.1	12.4	------	------	------	------
Washington Island.	1952	III	89	7.4	12.5	16.6	------	------	------
Minneapolis Shoals.	1952	III	162	6.9	11.6	15.5	------	------	------

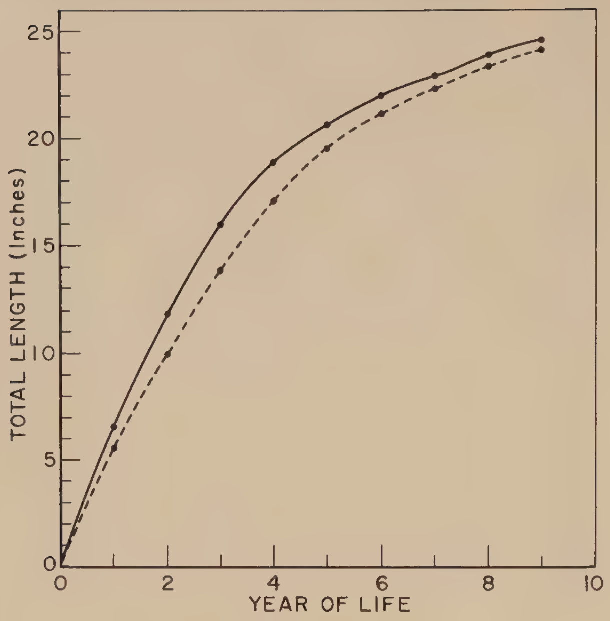


FIGURE 4.—Calculated length of whitefish from Lake Michigan (broken line) and central Green Bay (solid line).

The calculated lengths of members of the 1948 year class from Cedar River and Gills Rock agreed very well; the lengths were shorter at Washington Island than at the former localities and still shorter at Minneapolis Shoals (exception in second year of life).

Whitefish of the 1949 year class had slightly lower calculated lengths at Gills Rock than at Washington Island, a situation directly opposite that shown by the 1948 year class. No explanation can be offered for this disagreement between the data for two year classes from the same collections.

The data for whitefish from Minneapolis Shoals were consistent in that calculated lengths for both the 1948 and 1949 year classes ran lower than at other locations.

The general conclusion seems warranted that some real growth differences may exist among whitefish in different localities within central Green Bay. These differences probably are not large and most likely can be exceeded by year-to-year differences at a single locality. It appears valid, therefore, to combine the data for all Green Bay samples to describe the general character of growth in the area (table 18).

The calculated lengths of table 18, like those of the component samples, lack a trend toward systematic change with age, except for a slight tendency for the calculated lengths for the first 3 or 4 years of life first to decrease and then to increase with the age of the fish on which calculations were based. The agreement between estimates of general growth from grand average calculated lengths and from the summation of the grand average increments was good. The latter estimate was selected for the comparison of the growth of whitefish in Lake Michigan and central Green Bay (table 19; fig. 4).

The outstanding difference between the growth of whitefish in Lake Michigan and central Green Bay was the slower growth of the Lake Michigan fish for the earlier years of life and their more rapid growth in the later years. The situation is seen most clearly in the annual increments.

TABLE 18.—*Calculated total length of whitefish from central Green Bay waters*

[All collections combined]

Age group[1]	Number of fish	Calculated length at end of year of life								
		1	2	3	4	5	6	7	8	9
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
I	2	7.3								
II	100	7.1	12.3							
III	442	6.9	12.0	16.2						
IV	90	6.2	11.1	15.4	18.2					
V	33	6.4	11.7	15.2	17.9	19.1				
VI	114	5.8	11.0	15.1	18.3	20.2	21.6			
VII	2	8.3	12.9	17.5	20.1	21.7	22.8	23.8		
VIII	2	7.8	13.8	17.4	20.3	21.6	22.7	23.1	24.5	
IX	2	7.7	10.5	15.9	18.9	20.6	21.9	23.1	23.8	24.5
Grand average calculated length		6.6	11.8	15.8	18.2	20.0	21.7	23.3	24.1	24.5
Increment of average		6.6	5.2	4.0	2.4	1.8	1.7	1.6	.8	.4
Grand average increment of length		6.6	5.2	4.2	2.9	1.7	1.4	.9	1.0	.7
Sum of average increments		6.6	11.8	16.0	18.9	20.6	22.0	22.9	23.9	24.6

[1] Age groups of late-autumn samples have been combined with the next higher age groups of spring and summer samples.

TABLE 19.—*Calculated total length of whitefish from Lake Michigan and central Green Bay*

[Data from tables 8 and 18; based on successive addition of grand average increments]

Year of life	Lake Michigan		Green Bay		Difference of length	Ratio of increments
	Length	Increment	Length	Increment		
	Inches	*Inches*	*Inches*	*Inches*	*Inches*	
1	5.6	5.6	6.6	6.6	1.0	1.1
2	9.8	4.2	11.8	5.2	2.0	1.2
3	13.8	4.0	16.0	4.2	2.2	1.05
4	17.2	3.4	18.9	2.9	1.7	.8
5	19.6	2.4	20.6	1.7	1.0	.7
6	21.2	1.6	22.0	1.4	.8	.8
7	22.3	1.1	22.9	.9	.6	.8
8	23.3	1.0	23.9	1.0	.6	1.0
9	24.1	.8	24.6	.7	.5	.8

The increments for Lake Michigan whitefish were the shorter by 1.0 inch in both the first and second years of life and by 0.2 inch in the third. Subsequently the increments for Lake Michigan fish were greater than those for Green Bay fish with the single exception of the equal values of 1.0 inch for the eighth year. The ratio of the annual increment for Green Bay fish to that of Lake Michigan fish exceeded 1.0 the first 3 years and was 0.7–1.0 the next 6 years. This shift in the relation of the increments causes the growth curves to diverge to a maximum of 2.2 inches at the end of 3 years of life and then to converge until the Green Bay fish were the longer by only 0.5 inch at the end of 9 years.

Whitefish of both stocks attained the minimum legal length of 17 inches in the fourth growing season. Green Bay whitefish reached that length fairly early in the fourth year but those from Lake Michigan were not 17 inches long until near the close of the growing season.

CALCULATED GROWTH IN WEIGHT

The difference between linear growth in Lake Michigan and central Green Bay whitefish and differences in the length-weight relation are reflected in differences in general growth in weight (table 20; fig. 5).

Although the calculated weights were nearly the same at the end of the first year (0.9 ounce, Lake Michigan; 1.0 ounce, Green Bay), the Green Bay fish were the heavier by 3.7 ounces at the end of the second year. This advantage increased rapidly to 12.0 ounces at the end of 4 years, declined to 8.7 ounces at the end of 7, and then rose to the maximum of 12.2 ounces at the end of 9 years.

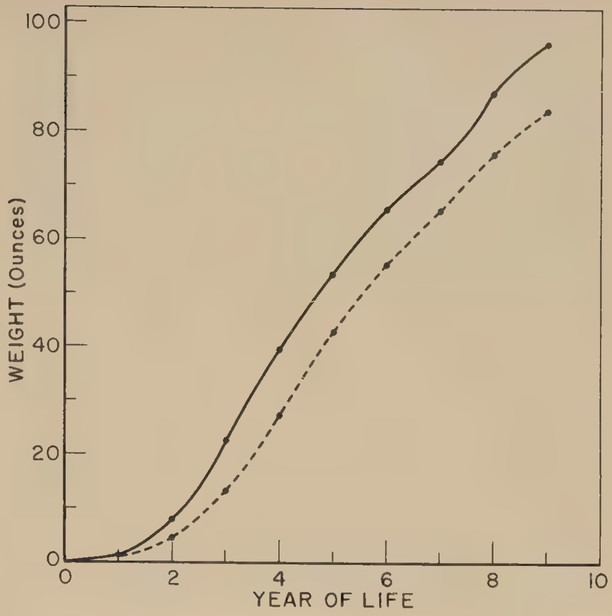


FIGURE 5.—Calculated growth in weight of whitefish from Lake Michigan (broken line) and central Green Bay (solid line).

TABLE 20.—*Calculated weight at the end of each year of life of whitefish from Lake Michigan and central Green Bay*

[Weights were computed from the calculated lengths of table 19 by means of the general length-weight equations]

Year of life	Lake Michigan		Green Bay		Difference of weight	Ratio of increments
	Weight	Increment	Weight	Increment		
	Ounces	*Ounces*	*Ounces*	*Ounces*	*Ounces*	
1	0.9	0.9	1.0	1.0	0.1	1.1
2	4.2	3.3	7.9	6.9	3.7	2.1
3	13.1	8.9	22.4	14.5	9.3	1.6
4	27.4	14.3	39.4	17.0	12.0	1.2
5	42.6	15.2	53.7	14.3	11.1	.9
6	55.4	12.8	65.9	12.2	10.5	.95
7	65.7	10.3	74.4	8.5	8.7	.8
8	76.1	10.4	87.3	12.9	11.2	1.2
9	84.0	7.9	96.2	8.9	12.2	1.1

The ratio of increments of weight showed the Green Bay fish to have greater annual growth in weight the first 4 years of life (low of 1.1 the first year and a high of 2.1 the second); the trend was reversed the next 3 years, when the Lake Michigan fish displayed greater annual increases. Increases for the Green Bay fish were again the greater in years 8 and 9. This relation differs from that of linear growth because once the Lake Michigan fish had the greater annual increments their increments continued to be the larger, with a single exception, for years 4 through 9.

The annual increments of weight of the Lake Michigan whitefish increased from 0.9 ounce at the end of the first year to a maximum of 15.2 ounces in the fifth and thereafter declined (except for the eighth) to 7.9 ounces in the ninth year. The increments of central Green Bay fish increased from the first-year value of 1.0 ounce to the fourth-year maximum of 17.0 ounces. The downward trend was then irregular; the lowest value was 8.5 ounces at the seventh year of life.

Without exception the Green Bay fish attained the weights of 1, 2, 3, 4, and 5 pounds in a year earlier than did the Lake Michigan fish (examples, 1 pound during third year in Green Bay and fourth in Lake Michigan; 3 pounds in fifth year in Green Bay and sixth in Lake Michigan; 5 pounds in eighth year in Green Bay and ninth in Lake Michigan).

The 2-pound size limit in effect in the State of Michigan waters of Green Bay at the time of sampling was reached by the Green Bay fish during the fourth year of life.

COMPARISON WITH GROWTH IN OTHER LAKE MICHIGAN WATERS

This section has been limited to the growth of whitefish in Lake Michigan since a full review and comparison of growth in the various Great Lakes waters was recently published by Dryer(1963). The data of table 21 are limited to the first 4 years of life, the period covered in the only previous publication on the growth of whitefish in Lake Michigan (Roelofs, 1958). Among the four areas for which growth data are now available, the South Fox Island fish had by far the poorest growth (only 13.2 inches at the end of 4 years). The central Green Bay fish grew the fastest; they were at least 1.0 inch longer than the others at any of the 4 years of life. Growth was similar in the Lake Michigan and Big Bay de Noc (northern Green Bay) areas. The calculated lengths were equal at 5.6 inches at the end of the first year and at 13.8 inches at the end of the third. The Lake Michigan fish were the longer at the end of 2 years (9.8 as compared to 9.4 inches) but the Bay de Noc fish were the larger (17.9 as compared to 17.2 inches) at 4 years.

The South Fox Island whitefish and the central Green Bay fish are different from each other and from both the Lake Michigan and Big Bay de Noc fish. The data offer no evidence, however, as to whether the growth rates of Lake Michigan and Big Bay de Noc fish are significantly different.

TABLE 21.—*Growth in total length of whitefish in differen parts of Lake Michigan*

Area and source of data	Calculated length at end of year of life			
	1	2	3	4
	Inches	*Inches*	*Inches*	*Inches*
Present study:				
Lake Michigan	5.6	9.8	13.8	17.
Central Green Bay	6.6	11.8	16.0	18.
Roelofs (1958):				
Big Bay de Noc	5.6	9.4	13.8	17.
South Fox Island	4.3	7.0	9.9	13.

SEX RATIO

The sex ratio ranged so widely from sample to sample (36 to 84 percent males—see bottom part of table 22) that it is extremely difficult to judge the possible effects of local and seasonal differences or gear selectivity.

Data on sex ratio often vary erratically when samples are collected near or during the spawning season. The strong preponderance of males in the October 1948 collections from Lake Michigan (77 percent) and Peshtigo (84 percent) might be attributed to prespawning segregation, but the equally great abundance of males (80 percent) in the June 1951 sample from Gills Rock makes this explanation much less attractive. The two collections made in late spring and early summer at Cedar River (45 and 48 percent males) agreed well. Agreement was good also between the July and September samples from Minneapolis Shoals (combined in table 22); the percentage of males was 59 in July and 60 in September. These two pairs of samples from the same locality, then, offer some evidence of local stability, within certain months at least. The only sample in which males were extremely scarce was taken in February 1952 at Washington Island.

Evidence is lacking for any effect of gear on the sex-ratio data. The two gill net samples had the highest (84 percent, Peshtigo) and the lowest (36 percent, Washington Island) percentages of males. The variation was wide also among the remaining samples, all from pound nets; here the percentage of males ranged from 45 (Cedar River) to 80 (Gills Rock).

It seems to be impossible also to speak of a trend in sex ratio with increase of age. A trend toward decrease in the percentage of males with increased age is clearly apparent in the Lake Michigan data but is lacking in the data for Cedar River, 1949—the other sample that covered a fair range of age groups. No clear trend can be established for the remaining samples.

TABLE 22.—*Sex composition of whitefish from Lake Michigan and central Green Bay*

Age and item	Lake Michigan October 1948	Peshtigo October 1948	Cedar River May 1949	Cedar River June 1951	Gills Rock June 1951	Washington Island February 1952	Minneapolis Shoals July and September 1952
group:							
Percentage males	100	-------	-------	-------	100	-------	100
Number of fish	(4)	-------	-------	-------	(1)	-------	(1)
I group:							
Percentage males	100	-------	33	-------	100	-------	51
Number of fish	(40)	-------	(3)	-------	(41)	-------	(59)
II group:							
Percentage males	100	100	50	48	70	33	63
Number of fish	(27)	(9)	(34)	(70)	(78)	(89)	(162)
V group:							
Percentage males	80	87	40	43	60	48	20
Number of fish	(20)	(37)	(15)	(7)	(5)	(21)	(5)
V group:							
Percentage males	61	76	67	0	-------	-------	-------
Number of fish	(106)	(29)	(3)	(1)	-------	-------	-------
VI group:							
Percentage males	33	-------	46	-------	-------	-------	-------
Number of fish	(3)	-------	(114)	-------	-------	-------	-------
VII group:							
Percentage males	-------	-------	50	-------	-------	-------	-------
Number of fish	-------	-------	(2)	-------	-------	-------	-------
VIII group:							
Percentage males	100	-------	0	-------	-------	-------	-------
Number of fish	(1)	-------	(2)	-------	-------	-------	-------
X group:							
Percentage males	-------	-------	100	-------	-------	-------	-------
Number of fish	-------	-------	(1)	-------	-------	-------	-------
Ages combined:							
Percentage males	77	84	45	48	80	36	60
Number of fish	(201)	(75)	(174)	(78)	(125)	(110)	(227)

The only conclusion warranted by the data of table 22 is that segregation by sex can be pronounced at times other than near the spawning period and/or that local differences in the sex ratio are extremely large.

AGE AND SIZE AT MATURITY

Usable data on both sex and maturity were available only for the Minneapolis Shoals collections of July and September 1952.

The single I-group male and all females of age group II were immature (table 23). Some males (16.7 percent) were mature as age group II and most males (87.3 percent) and a majority of the females (61.0 percent) were mature as age group III. The five IV-group whitefish (one male and four females; no older fish in the sample) all were mature.

All whitefish shorter than 14.5 inches were immature and all longer than 18.4 inches were mature. The first mature males appeared at 14.5–14.9 inches. The percentage of mature males reached 71.5 at 16.0–16.4 inches and was 100 percent above 18 inches (table 24). The first mature female appeared at 16.5–16.9 inches (2 inches longer than for the males); 68.7-percent maturity was reached at 17.0–17.4 inches and 100 percent above 18.4 inches (0.5 inch longer than for males). More than half of all fish of each sex were mature at all lengths, greater than the 17-inch size limit.

TABLE 23.—*Relation of age to maturity of whitefish taken at Minneapolis Shoals in July and September 1952*

[The single I-group male was immature; the 5 IV-group fish (1 male; 4 females) were all mature]

Sex and state of gonads	Age group II	Age group III
Male:		
Mature	5	90
Immature	25	13
Percentage mature	16.7	87.3
Female:		
Mature	0	36
Immature	29	23
Percentage mature	0.0	61.0

TABLE 24.—*Relation of total length (inches) to maturity of whitefish taken at Minneapolis Shoals in July and September 1952*

[All fish shorter than 14.5 inches were immature, and all longer than 18.4 inches were mature]

Length	Males		Females	
	Number of fish	Percentage mature	Number of fish	Percentage mature
14.5–14.9	6	16.7	4	0.0
15.0–15.4	11	9.0	8	.0
15.5–15.9	6	16.7	5	.0
16.0–16.4	7	71.5	7	.0
16.5–16.9	15	93.3	6	16.7
17.0–17.4	39	79.5	16	68.7
17.5–17.9	20	90.0	21	71.5
18.0–18.4	18	100.0	9	77.7

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LITERATURE CITED

BALDWIN, NORMAN S., AND ROBERT W. SAALFELD.
1962. Commercial fish production in the Great Lakes 1867–1960. Great Lakes Fishery Commission, Technical Report No. 3, 166 pp.

DEASON, HILARY J., AND RALPH HILE.
1947. Age and growth of the kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Transactions of the American Fisheries Society, vol. 74, for the year 1944, pp. 88–141.

Dryer, William R.

1963. Age and growth of the whitefish in Lake Superior. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 63, No. 1, pp. 77–95.

Edsall, Thomas A.

1960. Age and growth of the whitefish, *Coregonus clupeaformis*, of Munising Bay, Lake Superior. Transactions of the American Fisheries Society, vol. 89, No. 4, pp. 323–332.

Hart, John Lawson.

1931. The growth of the whitefish, *Coregonus clupeaformis* (Mitchill). Contributions to Canadian Biology and Fisheries, N.S., vol. 6, No. 20, pp. 427–444.

Hile, Ralph

1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. Transactions of the Wisconsin Academy of Science, Arts, and Letters, vol. 33, pp. 189–337.

1950. Green Bay walleyes—a report on the scientific investigation of the marked increase in abundance of walleyes in Green Bay. The Fisherman, vol. 18, No. 3, pp. 5–6. (Grand Haven, Mich.)

Hile, Ralph, and Howard J. Buettner.

1959. Fluctuations in the commercial fisheries of Saginaw Bay 1885–1956. U.S. Fish and Wildlife Service, Research Report No. 51, 38 pp.

Hile, Ralph, George F. Lunger, and Howard J. Buettner.

1953. Fluctuations in the fisheries of State of Michigan waters of Green Bay. U.S. Fish and Wildlife Service, Fishery Bulletin 75, vol. 54, pp. 1–34.

Moffett, James W.

1952. The study and interpretation of fish scales. The Science Counselor, vol. 15, No. 2, pp. 40–42.

Morawa, F.W.F.

1960. Jahreszeitliche Veränderungen der chemischen und gewichtsmässigen Zusammensetzung von *Coregonus fera* Jurine des Genfer Sees. Annales de la Station Centrale d'Hydrobiologie Appliquée, tome 8, pp. 281–306.

Pycha, Richard L.

1961. Recent changes in the walleye fishery of northern Green Bay and history of the 1943 year class. Transactions of the American Fisheries Society, vol. 90, No. 4, pp. 475–488.

Roelofs, Eugene W.

1958. Age and growth of whitefish, *Coregonus clupeaformis* (Mitchill), in Big Bay de Noc and northern Lake Michigan. Transactions of the American Fisheries Society, vol. 87, for the year 1957, pp. 190–199.

Smith, Stanford H.

1954. Method of producing impressions of fish scales without using heat. U.S. Fish and Wildlife Service, Progressive Fish-Culturist, vol. 16, No. 2, pp. 75–78.

Van Oosten, John.

1923. The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefishes of known ages. Zoologica, Scientific Contributions of the New York Zoological Society, vol. 2, No. 17, pp. 380–412.

1939. The age, growth, sexual maturity, and sex ratio of the common whitefish, *Coregonus clupeaformis* (Mitchill), of Lake Huron. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 24, for the year 1938, part 2, pp. 195–221.

Van Oosten, John, and Ralph Hile.

1949. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in Lake Erie. Transactions of the American Fisheries Society, vol. 77, for the year 1947, pp. 178–249.

FEEDING AND GROWTH OF JUVENILE SOFT-SHELL CLAMS, *MYA ARENARIA*

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ABSTRACT

Laboratory experiments and observations on the growth of juvenile clams, *Mya arenaria*, of known age were conducted to aid in developing artificial rearing procedures. Laboratory clams held in running natural sea water without supplemental food, or in standing water with supplemental food, grew as well or better than those in nearby clam flats. The only suitable foods for artificial feeding were species of unicellular algae. Population density affected growth chiefly through competition for food. Growth increased with temperature when food was adequate, although the winter decline in growth rate apparently was related to decreased food supply as well as to low temperature.

When clams were fed artificially, the concentration of food in the water was critical: concentrations of over 30,000 cells per ml. water led to inefficient utilization by the clams. Need for additional information on water pumping rates, duration of feeding activity, efficiency of food utilization, and the abundance and kinds of clam food in natural sea water is discussed.

Estimating the age of an organism is essential in studying its growth rate and calculating the potential yield of a population. The age of the soft-shell clam, *Mya arenaria*, is generally estimated by counting winter checks or annuli on the shells; however, this method may result in error because the first and possibly the second annulus is apt to be obscured or worn away. Judgement of the first year's growth often is based on experience gained from field observation of juvenile clams at different times of the year. These observations are apt to be misleading, for one seldom knows exactly when the small clams were spawned or whether they represent one or several spawnings, perhaps months apart. Small clams observed in midsummer could be either slow-growing individuals spawned the previous year or fast-growing individuals spawned in the current year. Furthermore, sampling procedures ordinarily used in field studies may introduce a bias leading to inaccurate estimates of size distribution. Unless the clam-bearing sediments are subjected to long and painstaking separation in the laboratory, the smallest individuals generally are missed. The customary practice of sieving the sediments in the field becomes impracticable with mesh small enough to retain the early postlarval juveniles.

Observations on the growth of clams of known age should provide a more accurate means of interpreting field data. In addition, a knowledge of early clam growth is valuable in planning artificial culture techniques. The artificial culture of shellfish, particularly the hatching and rearing of juveniles as "seed," has achieved worldwide interest in recent years. Although much of the current interest concerns species other than *Mya*, the artificial propagation of this clam frequently has been proposed as a management tool. Because economical artificial rearing demands rapid growth rates, the conditions favoring such growth and the factors limiting it should be understood.

The experiments described in the following pages were undertaken to determine whether juvenile

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clams could be reared under artificial conditions. Although primarily intended as guidelines for the development of rearing techniques, the results provided basic biological information about the early growth of clams. The purpose of this paper is to present (1) a standard of growth for clams of known age under laboratory conditions; (2) an evaluation of this standard (the degree to which it is representative of natural growth in various clam producing areas); and (3) information about environmental influence on growth.

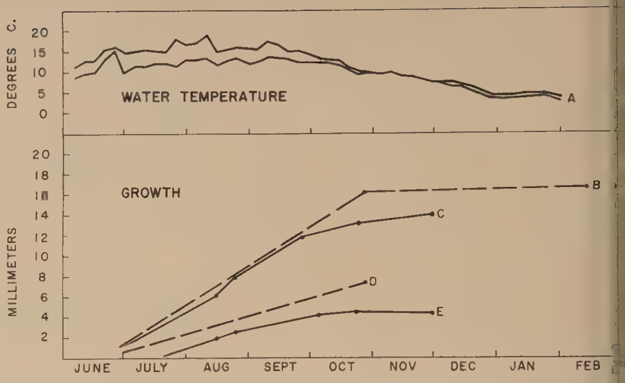

FIGURE 1.—Growth of laboratory reared clams in running sea water. Dash lines indicate lack of intervening measurements.

A. Five-day averages of maximum and minimum supply line water temperatures.
B. Growth of May 28 brood at a population density of less than one clam per 5 cm.^{2}.
C. Same as (B), except disturbed periodically for measurement.
D. Growth of May 28 brood at a population density of more than one clam per cm.^{2}.
E. Growth of June 20 brood at a population density of more than one clam per cm.^{2}.

METHODS

The growth experiments described in this paper utilized clams of known age, having been spawned and reared in the laboratory. Clams used in any one experiment were from the same brood (i.e., all spawned at the same time, but not necessarily from the same parents). Some of the clams were held in natural running sea water, while others were subjected to experimental treatments in both running and standing sea water. When standing sea water was used, periodic changes of the water and artificial feeding were necessary. These conditions provided better control of some environmental factors, such as food supply, than did the use of running water.

Except where temperature was itself the variable under investigation, all experiments were conducted at prevailing seasonal temperatures; that of the sea water in the supply lines (fig. 1, A) or of the ambient air in the laboratory. Laboratory air temperatures, which determined the temperature of most standing water experiments, ranged from 18° to 22° C. in summer and from 14° to 17° C. in winter. Water temperatures were varied by immersing standing-water containers in a water bath. Running water was heated or cooled by passing the incoming water through a heat exchanger. In early experiments, these heat exchangers were polyethylene cylinders equipped with electric immersion heaters or a refrigerator coil controlled by thermostats. For Experiment 7, a specially engineered control system provided desired flow rates and temperatures.

Growth, the criterion used to evaluate the effects of experimental treatment, was determined by measuring the shell length before and after treatment. Clams over 2 mm. long were measured with vernier calipers, those less than 2 mm., with an ocular micrometer. In Experiment 2, the number of clams was large and the individuals were small and difficult to measure; therefore, some of the initial and terminal mean sizes were estimated from samples rather than from measurements of all individuals. These estimates and the mean growth derived from them were subject to sampling error. However, the estimated mean sizes plus or minus two standard errors were found reliable at a confidence level of 95 percent or better. For growth means (the difference between initial and terminal mean sizes) with this degree of reliability the following confidence limits were assigned: the lower limit was the difference between the terminal mean size less two standard errors and the initial mean size plus two standard errors; the upper limit was the difference between the terminal mean size plus two standard errors and the initial mean size less two standard errors. When only the initial mean size was estimated from a sample and the terminal mean size was determined by measuring every individual, the 95 percent confidence interval was reduced by about one-half. When all the clams were measured, before and after the treatment period, sampling error was not involved.

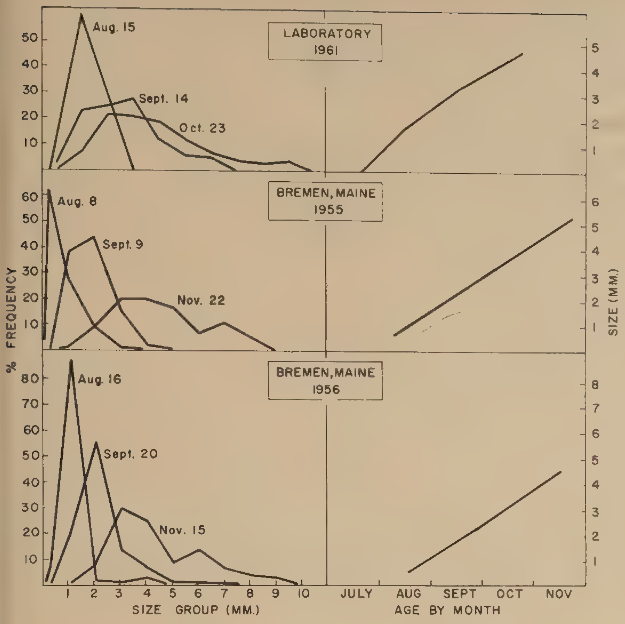

Figure 2.—Size-frequency distributions and mean lengths of laboratory and natural clam populations at monthly intervals.

Except when held in running water, clams were fed suspensions of unicellular algae of known volume and measured for cell concentration with a haemocytometer. When dry-weight values of the food supply were desired, 10 volumetric samples of the food suspension were filtered, washed, dried, and weighed, and the mean weight converted to dry weight per million cells.

RESULTS

Concurrently with the experiments described below, the broods providing the experimental clams were held in containers of running sea water and were not disturbed except for occasional measurings. The population density under these conditions was relatively high—in excess of one clam per cm.^{2}; therefore, a portion of one brood was removed and held at a much lower density (about one clam per 5 cm.^{2}) for comparative observation. The growth of these clams, reflecting the most elementary sort of laboratory culture, served as a guide for evaluating growth under more artificial conditions. Dense populations grew more slowly than populations from the same brood held at reduced density. Growth was slightly better when the clams were not disturbed than when they were removed periodically for measurements. The optimum growth rate achieved averaged about 3.8 mm. per month. The growth rate in the high density populations averaged about 1.8 mm. per month. Growth in all groups became slower during the fall, and virtually ceased in the winter. The comparative growth rates are shown in figure 1. The size-frequency distributions of a dense population (that shown in figure 1, E) at each measurement period are shown in figure 2, top left.

EXPERIMENT 1

Effect on Growth of Competition Between Fast and Slow Growing Individuals

The size frequency distribution of young clams of the same age changes as the clams grow, reflecting an increase in range and skewness. The large individuals grow faster than the smaller ones. Not only does the growth increment per unit time increase with size, but this increment as a fraction of the total length also increases. The nonlinearity of the early growth rate skews the distribution curve to the right. Although this is a recognized attribute of early growth in many organisms, it seemed possible that the phenomenon also was influenced by interaction among the clams. Thus, if the food gathering ability of the individuals increased with size, fast growing clams might grow even faster at the expense of the others. To test this experimentally, two sizes of clams were distributed in 200-ml. glass finger bowls of filtered sea water:

(1) Bowls 1 and 2 with 50 "small" (about 1.2 mm.) clams each.

(2) Bowls 3 and 4 with 5 "large" (about 2.6 mm.) clams each.

(3) Bowls 5 and 6 with 4 "large" and 10 "small" clams each.

The individual and mean sizes of the "large" and "small" clams in each bowl were recorded. The relative numbers of "large" and "small" clams assigned to each bowl were determined on the basis of the cube of their length: one "large" clam was assumed equivalent to 10 small ones. Thus, the total food requirement for each bowl was considered equal. The mean daily ration was 35.9×10^6 algal cells (*Dicrateria* sp. and *Monochrysis lutheri*) per bowl. After 27 days, the clams were measured and the mean growth of both "large" and "small" clams determined (table 1).

The similarity in growth between "small" clams with and without competition from the larger, and also between the "large" clams with and without the competition of the smaller, indicates that interaction between clams of different sizes does not have a more appreciable effect on the growth rate than competition between clams of similar sizes.

TABLE 1.—*Growth of juvenile clams in populations of uniform and of mixed sizes*

Experimental group	Initial size	Terminal size	Growth
	Millimeters	*Millimeters*	*Millimeters*
"Large" clams only	2.5	6.7	4.2
"Large" clams only	2.6	6.7	4.1
"Small" clams only	1.1	3.1	2.0
"Small" clams only	1.2	3.0	1.8
"Large" clams in mixed populations	2.7	6.7	4.0
"Large" clams in mixed populations	2.8	6.4	3.6
"Small" clams in mixed populations	1.2	3.3	2.1
"Small" clams in mixed populations	1.2	3.1	1.9

EXPERIMENT 2

Effect of Population Density on Growth

Although the effects of reducing population density are apparent (fig. 1), a more precise test was desirable, particularly to ascertain whether the effects were associated with density in some way other than in competition for food. The mean size of the clams in the December 1 brood was estimated from a sample of 127 individuals on February 9. From this brood, 1,480 individuals were distributed among 16 glass bowls, each containing 200 ml. of filtered sea water, so that one series of four bowls contained 200 clams each; a second series, 100 clams each; a third series, 50 clams each; and a fourth series, 20 clams each. To facilitate feeding and handling, the physical positions of the bowls were not randomized, but arranged in a square of four rows of 4 bowls at each population density. The clams composing the population of each bowl were selected at random. The initial mean size of the clams in all but the last 4 bowls was assumed to be that of the brood mean plus or minus two standard errors. The initial mean size of the clams in the last 4 bowls was determined by measuring all individuals. Food (*Dicrateria* sp.) was supplied twice daily in measured quantities, so that one bowl in each series received twice that of the second bowl, 4 times that of the third bowl and 8 times that of the fourth. Thus a range of feeding rates (food available per clam) was obtained. This range included several duplications of feeding rates resulting from different combinations of food supply and numbers of individuals to share it. Twenty-four days later, the clams were again measured. From the four high-density bowls, randomly selected samples of 100 individuals were measured; from the other bowls, all of the clams were measured (table 2 and fig. 3).

TABLE 2.—*Effects of competition on the growth and size distribution of juvenile clams*

Bowl number	Clams used	Food		Mean size		Growth	
		Cells supplied	Cells per clam	Initial	Terminal	Absolute	Relative
	Number	*Millions*	*Millions*	*Millimeters*	*Millimeters*	*Millimeters*	*Millimeters*
1	200	992	4.96	1.62	2.08	0.46	0.09
2	200	496	2.48	1.62	2.09	.47	.19
3	200	248	1.24	1.62	1.93	.31	.25
4	200	124	.62	1.62	1.99	.37	.59
5	100	992	9.92	1.62	2.26	.64	.06
6	100	496	4.96	1.62	2.02	.40	.08
7	100	248	2.48	1.62	1.92	.30	.12
8	100	124	1.24	1.62	1.87	.25	.20
9	50	992	19.84	1.62	2.48	.86	.04
10	50	496	9.92	1.62	2.35	.73	.07
11	50	248	4.96	1.62	2.08	.46	.09
12	50	124	2.48	1.62	1.90	.28	.11
13	20	992	49.6	1.52	2.60	1.08	.02
14	20	496	24.8	1.65	2.41	.76	.03
15	20	248	12.4	1.41	2.16	.75	.06
16	20	124	6.2	1.47	1.66	.19	.03

As expected, growth was inversely proportional to population density and directly proportional to the amount of food supplied, although this relationship did not appear significant at the highest population density. These results could be related to competition for food alone, or to competition for food plus other density dependent effects. In almost every instance, however, where the amount of food per clam was similar and the population density was different, growth showed no consistent or significant relationship to the density. This can be seen by tracing the positions of corresponding geometrical symbols across figure 3. Here only the three highest population densities are considered, since among these are several cases of duplication or triplication of feeding rates. Feeding rates of 1.24×10^6 cells per clam occurred in bowls 3 and 8; rates of 2.48×10^6 cells per clam occurred in bowls 2, 7, and 12; rates of 4.96×10^6 cells per clam in bowls 1, 6, and 11; and rates of 9.92×10^6 cells per clam in bowls 5 and 10. These feeding rates are indicated in the graph by crosses, squares, circles and triangles, respectively. In no case is there a consistent or significant slope to the lines determined by corresponding symbols.

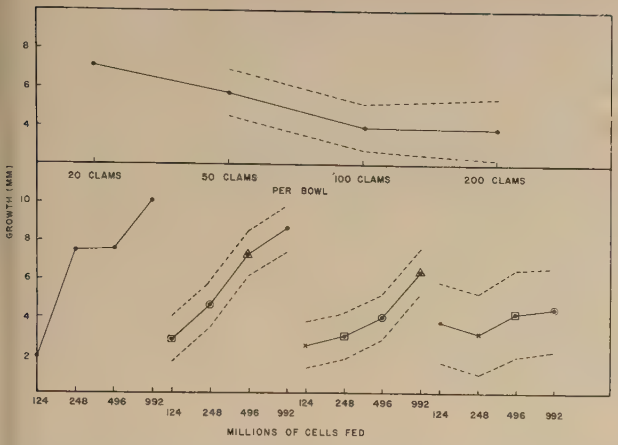

FIGURE 3.—Top: relation between population density and growth. Each point represents the mean growth in all bowls at each population density. Bottom: relation between available food and growth at the four population densities designated above. Corresponding geometrical symbols represent equivalent feeding rates (number of cells available per clam). Dash lines indicate 95 percent confidence limits.

One instructive feature of the data obtained from this experiment is the mean growth plotted against feeding rate (fig. 4). The growth, which increases with feeding rate, does not increase linearly. The growth per unit of food (table 3, last column) is lower at a high feeding rate than at a low feeding rate. This phenomenon suggests inefficient utilization of food at high concentrations. The method of feeding may be partly responsible for this effect. Food was introduced twice daily and, immediately following its introduction, the concentration of cells was highest in the maximally fed bowls. Here the concentration averaged about 145×10³ cells per ml., substantially higher than clams normally encounter in nature. Had the same amount of food been introduced in smaller quantities at more frequent intervals, the feeding efficiency of the maximally fed clams might have been improved. Some effects of cell concentration on feeding efficiency are described below.

EXPERIMENT 3

Effect of Food Concentration on Feeding Efficiency

Under certain conditions, clams reject masses of particles filtered from the water instead of ingesting them. The presence of these masses (pseudofeces) among the true fecal material in the containers indicates inefficient food utilization.

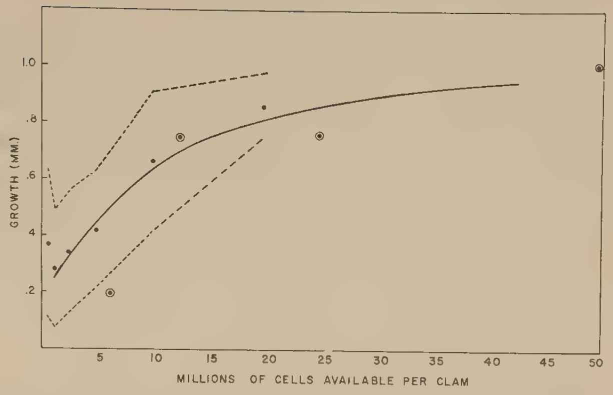

FIGURE 4.—Relationship between growth and feeding rate. Solid points represent estimates based on sampling, for which the 95 percent confidence limits are designated by dash lines. Circled points represent means obtained from measuring entire groups of clams. The curve (solid line) has been fitted by eye.

To determine the effect of food concentration on the amount of pseudofeces produced, food was supplied in different initial concentrations. Four pairs of bowls, each containing five clams (averaging 8.0 mm.) and 200 ml. of filtered sea water were provided with *Dicrateria* cells according to the following schedule:

(1) First pair fed 90×10⁶ cells once in 8 hours.

(2) Second pair fed 45×10⁶ cells twice in 8 hours.

(3) Third pair fed 18×10⁶ cells five times in 8 hours.

(4) Fourth pair fed 9×10⁶ cells 10 times in 8 hours.

All groups, therefore, received the same amount of food, but the initial concentrations of cells in the water were different: 450×10³, 225×10³, 100×10³, and 50×10³ cells per ml., respectively. After 8 hours the material accumulated in the bowls was examined under the microscope. Much of the food had been rejected as pseudofeces except in those bowls where the concentration immediately after feeding was less than 100×10³ cells per ml.

EXPERIMENT 4

Effect of Food Concentration on Digestive Efficiency

Food particles ingested and passed through the gut sometimes were not digested, and the presence of intact algal cells in the feces also indicated inefficient food utilization. The effect of cell concentration on this type of inefficiency was

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investigated in an experiment similar to the preceding one. Four pairs of bowls, each containing five clams (averaging 16.5 mm. in size) and 1,000 ml. of filtered sea water were provided with *Dicrateria* cells on the following schedule:

(1) First pair fed 136×10^6 cells once in 8 hours.

(2) Second pair fed 68×10^6 cells twice in 8 hours.

(3) Third pair fed 27.2×10^6 cells five times in 8 hours.

(4) Fourth pair fed 13.6×10^6 cells 10 times in 8 hours.

The initial concentrations therefore were 136×10^3, 68×10^3, 27.2×10^3, and 13.6×10^3 cells per ml., respectively. Examined after 8 hours, the feces in the first and second pairs of bowls contained substantial quantities of undigested cells. In the third pair, fewer undigested cells were present, but only in the fourth pair was the amount negligible. Therefore, at concentrations greater than about 30×10^3 cells per ml., inefficiency of food utilization occurs due to incomplete digestion. Although concentrations of this magnitude are not frequent in the natural environment, they might occur in laboratory clam culture through misguided attempts to force growth. Not only do moderately high concentrations result in poor efficiency, but very high concentrations may inhibit feeding almost entirely (Blake, 1961).

EXPERIMENT 5

Relationship Between Quantity of Food Eaten and Growth

Several attempts were made to relate growth to the quantity (weight) of food eaten. Experimental and control groups of clams were measured and placed in separate bowls, each containing 200 ml. of filtered sea water. The experimental groups were provided with measured quantities of *Dicrateria* cells twice daily, while control groups were fed nothing. After a few weeks the mean growth was determined (table 3). This value was corrected for growth not due to the food supplied, by subtracting the mean growth of the controls. The corrected mean growth was then converted to a monthly basis. The numbers and sizes of the clams, the amount of food provided, and the duration of each experiment are recorded in table 3. In the third group, the 25 experimental clams were divided equally among 5 bowls, rather than held all in one bowl as with the other groups.

The growth rates for 5 mm. clams were 2.7 an
3.0 mm. per month, respectively—rates similar t
those observed in running water at low populatio
density. Although the quantities of food su
plied were accurately measured, it was not possibl
to determine how much of this was actually eate
and digested. Since the cell concentration in
mediately after feeding in these experiments w
high (0.2×10^6–0.3×10^6 cells per ml.) some i
efficiency in utilization probably occurred and th
actual consumption of food probably was le
than indicated.

In this experiment, as with most of the other
Dicrateria sp. was used as food. Experiments t
evaluate other algal species showed that a diatom
Cyclotella nana, was slightly better, and a flage
late, *Monochrysis lutheri*, was slightly poore
Still poorer, but not unsatisfactory, foods we
Phaeodactylum tricornutum and *Olithodiscus* s
Chlorella sp. and *Tetraselmis* sp. promoted ver
little growth. No growth was obtained by feedin
nonliving food materials such as pulverized se
weeds (*Fucus* and *Ulva*), flour, tomato juice, an
dehydrated dogfood or mouse food.

TABLE 3.—*Growth data for artificially fed clams in exper*
ment 5

	First group		Second group		Third group	
	Experimental	Control	Experimental	Control	Experimental	Con-trol
Number of clams	20	20	10	10	25	5
Mean initial length (mm.)	2.36	2.32	5.02	5.02	5.40	5.
Mean terminal length (mm.)	3.90	2.37	6.96	5.11	7.60	5.
Observed increase (mm.)	1.54	.05	1.94	.09	2.20	.
Corrected increase (mm.)	1.49	--------	1.85	--------	1.80	------
Millions of cells supplied/day/clam	2.49	--------	9.77	--------	8.01	------
Dry weight of cells supplied (mg./day/clam)	.03	--------	.11	--------	.21	------
Duration of experiment (days)	28	--------	20	--------	18	------
Growth in mm./month (30 days)	1.5	--------	2.7	--------	3.0	------

EXPERIMENT 6

Effect of Temperature on Growth

Observations on juvenile clams in runnin
natural sea water, and otherwise unfed, showe
that the growth rate declined in autumn an
virtually ceased in winter. Several experiment
were conducted to learn the effects of temperatur
on growth. The first of these were in Decembe
and January. Two groups of 60 small clams each
were held in running sea water (about 20 l. pe

hour), one group at the seasonal temperature of ° C., and the other at an average temperature of bout 19° C. Preliminary trials indicated that s long as the flow rate exceeded the combined umping rates of the clams, variations in flow ate had no appreciable effect on growth. A hird group of 65 individuals was held in standing vater, which was cooled in a sea-water bath to an verage temperature of 8° C. These clams were ed a daily ration of *Monochrysis lutheri*. After 1 month the fed clams showed a mean growth of .7 mm. Those in running water showed negigible growth at either temperature level (table 4).

ABLE 4.—*Effect of temperature on the growth of juvenile clams*

Season	Mean water temperature	Clams used	Mean size		Duration of experiment	Growth per month
			Initial	Terminal		
	° *C.*	*Number*	*Millimeters*	*Millimeters*	*Days*	*Millimeters*
ummer: In running natural sea water.	6	16	11.28	11.56	22	0.38
	12.5	16	11.31	12.35	22	1.42
	20	16	11.33	12.79	22	1.99
inter: In running natural sea water.	6	60	9.9	9.9	31	--------
	19	60	9.6	9.7	31	.1
n standing water, artificially fed.	8	65	10.7	11.4	32	.7

EXPERIMENT 7

xperiment Conducted the Following September

Three groups of 16 clams were held in running ea water at mean temperatures of 6°, 12°, and 20° ., the flow rates of the water being equal. After weeks, increases in mean size at the temperatures ited were 0.28, 1.04, and 1.46 mm., respectively table 4).

In summer, growth occurred at all temperatures ut was better in warmer water. In winter, ttle or no growth occurred in either warm or cold atural water, but did occur in cold water when upplementary food was provided. Therefore, eduction of temperature does reduce growth, but ith adequate food, some growth can occur in old water. Furthermore, as little growth was chieved during winter in either warm or cold naural water, the winter decline in growth is probbly due to a paucity of food in the water.

DISCUSSION AND CONCLUSIONS

To compare natural and laboratory growth of lams, data obtained in the field are necessary, but r reasons stated earlier, these data are difficult o obtain. Fortunately, some dependable data were available, taken from samples collected and processed in such a way that unbiased representation of all size groups was assured. These samples were collected during years when the setting period was comparatively short. Bias due to continued recruitment of small, postlarval sizes therefore was minimal. The samples were obtained in the late summer and autumn of 1955 and 1956 from a small cove near Bremen, Maine, a location typical of the Maine coast. In both years, the growth rate and size distribution were similar and not greatly different from those observed subsequently in the laboratory (fig. 2).

A comparison of the three sets of size and growth data reveals that, during the first months, the Bremen clams have slower growth and a narrower range of sizes than the laboratory clams. This may be due to some continued recruitment from the plankton prior to sampling. If so, the first month's growth would be faster than indicated by the data, and the almost linear growth curves for the field samples would be more convex, resembling the laboratory growth more closely.

Growth in other regions could be expected to differ—to be more rapid, for example, in the southern part of the range. Data from Mead and Barnes (1905) seem to demonstrate more rapid growth in southern areas, although their samples probably were biased by the errors previously mentioned, particularly since their sampling was done with "a rather coarse sieve." According to their report, the mean size of clams sampled in upper Narragansett Bay, R.I., increased from 6.1 mm. on July 4 to 23.7 mm. on September 30, an apparent mean growth of about 6 mm. per month. More recent data for southern New England is given by Matthiessen (1960), who measured the growth of marked clams held in trays in a Martha's Vineyard, Mass., salt pond. The smallest of these clams, 15–20 mm. in size, although not specifically aged, were probably the current year's juveniles and were growing at a rate of about 5 mm. per month in September.

The laboratory growth of clams at Boothbay Harbor was markedly better than natural growth when the laboratory clams were held at low population densities. A comparison between the growth of artificially fed clams and either natural growth or laboratory growth in running water is rather difficult, however. The environments, particularly the food supply, are not readily comparable. Adequate data, from the literature or from these experiments, are not available to place values on several important parameters necessary for this comparison. The amounts and kinds of food present in sea water, the pumping rates of the clams, the time actually spent in feeding, and the efficiency of food utilization are too imperfectly known. Nevertheless, growth as good or better than that obtaining in Maine coastal water was achieved by artificial feeding at a rate of 0.2 mg. of food daily per 5 mm. clam, and probably could have been achieved with even less food.

The greatest divergence of artificial feeding from natural conditions seemed to be in the rate and method of supplying food rather than the actual quantity or kind supplied. In nature, clams obtain adequate food by filtering large volumes of water containing sparsely dispersed particles. Artificial feeding permits the increase of food concentration, so that the clams may remove much greater quantities at the same filtering rate; however, the intermittent feeding used in the preceding experiments eliminates much of this advantage. In the first place, high initial concentrations are rapidly and wastefully reduced; secondly, residual concentrations between feedings may become too low for adequate nourishment, and energy used in continued water filtering is wasted. More natural conditions and better growth would probably be achieved by frequent or continuous feeding to maintain a more constant food concentration, not exceeding about 30,000 cells per ml.

The detrimental effects of crowding are apparent from the experimental results and are probably related largely to competition for food. Optimum population densities, therefore, would depend on the amount of food available, the water circulation, and the sizes of the clams.

Temperature also has an effect on growth, probably through its effect on water filtering rate. Although growth slows down appreciably in winter, this effect is caused by a decrease in food material in the sea water as well as by a reduction in the water filtration rate. The reduction in growth rate with temperature is not linear. The experimental data show that between 12.5° and 20° C., the rate per month decreases an average of 0.08 mm. per degree of temperatu drop. Between 6° and 12.5°, the rate decreas an average of 0.16 mm. per degree, about twice a much. This decrease extrapolated would indica cessation of growth at 3.7° C. According t Belding (1930), clams cease feeding entirely a 2.8° C.

These growth rates are based on the availabilit of food in summer. During the winter, growt ceases at higher temperatures, presumably due t a decrease in the phytoplankton content of th water. When this paucity of natural food w compensated by artificial feeding, the observe growth at a mean temperature of 8° C. was 0 mm. per month, almost the same as the expecte summer growth calculated at 0.16 mm. per degr above 3.7°.

In conclusion, the results of the laborator observations supported by the best available fiel data show that the first summer's growth of youn clams in a densely seeded Maine clam flat (an probably in other northern New England area as well) averages about 5 mm. and seldom excee 10 mm. Where the clams are more thinly dispersed or where hydrographic conditions ar highly favorable, these values may be greate In southern New England, warmer summer wate temperatures (20°–27° C.) may permit faste growth and a longer growing season.

LITERATURE CITED

Belding, David L.

1930. The soft-shelled clam fishery of Massachusett Commonwealth of Massachusetts, Department o Conservation, Division of Fish and Game, Marin Fisheries Section, Marine Fisheries Series No. 65 pp.

Blake, John W.

1961. Preliminary measurements of filter feedin activity of the soft-shell clam, *Mya arenaria*, by th use of radioactive algae. Biological Bulletin, vo 121, No. 2, p. 383.

Matthiessen, George C.

1960. Observations on the ecology of the soft clam *Mya arenaria*, in a salt pond. Limnology an Oceanography, vol. 5, No. 3, pp. 291–300.

Mead, A. D., and E. W. Barnes.

1905. Observations on the soft-shell clam. (Fift paper.) Thirty-fourth Annual Report of th Commissioners of Inland Fisheries of Rhod Island, pp. 30–68.

COMBINED EFFECTS OF TEMPERATURE AND SALINITY ON DEVELOPMENT OF EGGS AND GROWTH OF LARVAE OF *M. MERCENARIA* AND *C. VIRGINICA*

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ABSTRACT

A study of the effect of temperature on the survival and growth of larvae of the hard clam (*Mercenaria mercenaria*) and American oyster (*Crassostrea virginica*) has shown that the rate of growth of these larvae at different temperatures was critically affected by the type of food organisms available. Both clam and oyster larvae were able to utilize naked algae, such as the chrysophytes *Monochrysis lutheri, Isochrysis galbana* and *Dicrateria* sp., and show significant growth at lower temperatures than those at which chlorophytes, such as *Chlorella* sp., which have cell walls, could be utilized. This implies that the enzyme systems required to digest naked flagellates are active at lower temperatures than are the enzyme systems required to digest cell walls.

The cells of *I. galbana* and *M. lutheri* are destroyed by temperatures of 27.5° C.–30.0° C., and growth of larvae receiving these foods at such temperatures was reduced. *Chlorella* sp. can tolerate temperatures of 33.0° C., and the rate of growth of larvae receiving *Chlorella* sp. continued to increase with each 2.5° C. increase in temperature up to 33.0° C.

Salinity also affects the temperature tolerance of clam and oyster larvae. At near optimum salinities the larvae survive and grow over a significantly wider range of temperatures than at salinities near the lower limits of their tolerance. We observed the temperature tolerances of clam and oyster larvae at a series of decreased salinities.

The development of comparatively routine methods for rearing lamellibranch larvae (Loosanoff and Davis, 1950) allowed a number of studies on the effect of various environmental factors on the development of eggs and on the survival and growth of larvae of bivalve mollusks. These studies have, in general, been conducted by varying the one factor under observation, while holding other factors as constant as possible.

Although we have reared the larvae of 20 species of lamellibranchs, at the Bureau of Commercial Fisheries Biological Laboratory in Milford, Conn., we confined experiments on the tolerances of larvae to environmental factors to two species, the American oyster, *Crassostrea virginica*, and the hard clam, *Mercenaria* (=*Venus*) *mercenaria*. We studied the effects, upon the eggs and larvae of these species, of turbidity, salinity, temperature, the kind and quantity of food, the concentration of eggs and larvae, and a variety of dissolved materials (Loosanoff and Davis, 1963).

Informative as such studies were, the results might not apply absolutely to these organisms in nature where more factors must be considered. We know little about the combined effect of two or more environmental factors on lamellibranchs. Medcof and Needler (1941) attempted to deduce the interaction of temperature and salinity on the condition index of oysters, *C. virginica*, in natural waters, and Costlow, Brookhout, and Monroe (1960, 1962) have obtained laboratory data on the combined effects of temperature and salinity on development of eggs and larvae of the decapod crustaceans *Sesarma cinereum* and *Panopeus herbstii*. Kinne (1963) has reviewed the present

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knowledge of the effects of temperature and salinity on marine and brackish water fish and has emphasized the fact (p. 302) that "monofactorial analysis may lead to conclusions that are ecologically invalid," and "should be replaced wherever possible by bi, tri or polyfactorial approach." We undertook the present study to determine how variations in such factors as food and salinity affected the temperature tolerance of eggs and larvae of the American oyster, *C. virginica*, and the hard clam, *M. mercenaria*.

METHODS

Adult clams and oysters were induced to spawn in the laboratory. Induction was by thermal stimulation and the addition of a water suspension of ripe gametes as previously described (Loosanoff and Davis, 1963). To determine the effects of experimental conditions on development of eggs, 10,000 to 15,000 recently fertilized eggs were placed in each 1-liter beaker. To determine the effects of the same conditions on survival and growth of larvae, three to six 15-liter cultures, each containing approximately 500,000 eggs, were started using our normal sea water (salinity 27.5 parts per thousand (p.p.t.)) at 24.0°±1.0° C. After 48 hours the eggs developed into normal straight-hinge larvae. These larvae were then screened from all containers and resuspended in a single 4-liter container. We measured the number of larvae per unit volume and placed the desired number of larvae (usually 8,000 to 15,000) in each of the 1-liter beakers.

In preliminary experiments to find the effects of different food organisms on survival and growth of larvae at different temperatures, duplicate cultures of 48-hour larvae were set up for each food, or combination of foods, and replicate sets were prepared for each of the six different temperatures tested in a single experiment.

In the experiments to study the combined effects of temperature and salinity on egg development and on survival and growth of larvae, duplicate cultures of eggs were established in each of the six salinities tested and replicate sets were prepared for each of the six different temperatures tested, giving a total of 72 cultures in each experiment.

To learn the effect of the several combinations of salinity and temperature on egg development 48 hours after the eggs were placed in the experimental cultures, the larvae in each culture were collected, on a stainless steel screen of small enough mesh to retain them, and resuspended in a 250-ml. graduated cylinder. After thoroughly mixing them, we withdrew and preserved a 4-ml. quantitative sample. We examined these samples under a compound microscope (×110) and counted the eggs developing into normal living larvae. To compare the numbers developing normally in successive experiments, we tabulated the results as a percentage of the maximum number developing under any combination of temperature and salinity in that experiment.

In experiments to determine the combined effect of temperature and salinity on survival and growth of larvae, we changed the water in the cultures every second day to eliminate waste products of larval metabolism and reestablish experimental conditions. In most of our work we added supplemental food daily (Davis and Guillard, 1958), but to keep our salinities constant in the experiments involving reduced salinities, we added food only every second day, when the water was changed and the salinities were adjusted.

To determine the percent survival and growth rate of clam larvae, after 10 days at the experimental conditions or when the larvae were 12 days old we took quantitative samples, in a manner similar to that used at 48 hours. The majority of larvae kept at or near optimum conditions had reached setting size by this time, but even those that had metamorphosed were collected on the screen, resuspended, and included in the quantitative samples.

We took samples for comparing growth rates and survival of oyster larvae after 8 days of experimental treatment or when the larvae were 10 days old. Under optimum conditions, some of the larvae were setting between the 10th and 12th days. Since recently metamorphosed oysters cannot be collected on the screen and resuspended, a random quantitative sample cannot be taken once setting starts.

We examined separate preserved samples under a compound microscope, and counted the larvae that survived the experiment. In addition, we measured 50 clam larvae or 100 oyster larvae from each sample, and calculated the increase in mean length during the experiment as a percentage of the increase in size of larvae in the most rapidly growing culture.

RESULTS

Type of Food and Growth of Larvae at Different Temperatures

Previous experience had indicated that the failure of larvae to grow at 30.0° C. in some experiments might be an indirect effect of the temperature on the marine algae used as foods rather than a direct effect on the larvae themselves. This was supported by Ukeles (1961) who reported that the cells of the chrysomonads *Isochrysis galbana* and *Monochrysis lutheri*, the two food organisms used in these early experiments, were destroyed by temperatures above 27.0° C.

Because we were interested in determining the direct effects of temperature and salinity on larvae, we designed preliminary experiments to demonstrate the effect of different foods on growth of larvae at different temperatures. In the first experiment, we kept oyster larvae at temperatures of 10.0°, 15.0°, 20.0°, 25.0°, 30.0°, and 33.0° C. with one culture at each temperature receiving *Dunaliella euchlora*, another *Chlorella* sp. (580),[1] and the third a mixture of *Chlorella* sp. (580), *Dicrateria* sp. (BII),[2] *I. galbana* and *M. lutheri*. The results are shown in figure 1. At 10.0° and 15.0° C. the larvae did not grow appreciably on any of these three foods. At 20.0° C., however, larvae fed the mixture of algae grew appreciably but those receiving the motile green chlorophyte, *D. euchlora*, showed only slight growth and larvae given only the nonmotile chlorophyte, *Chlorella* sp. (580), which has a distinct cell wall, grew hardly at all.

Above 20.0° C., the growth rate of larvae receiving *Chlorella* sp. (580) increased with each increase in temperature. The growth rate of larvae receiving *D. euchlora*, on the other hand, was similar at 25.0°, 30.0°, and 33.0° C., and the growth rate of larvae receiving the mixed algae increased progressively only up to 30.0° C. At 33.0° C., the growth rate was somewhat slower than at 30.0° C.

A second experiment was run to clarify the upper and lower temperature limits for growth of oyster larvae (fig. 2). Again, larvae fed the mixture of algae and kept at 15.0° C. did not grow. Growth of larvae kept at 17.5° C. was minimal, but at 20.0° C. the larvae grew faster, although at 10 days these larvae were still much smaller than those kept at 30.0° or 33.0° C. At 35.0° C., the rate of growth was also much slower than at 30.0° or 33.0° C. and all the larvae died before the end of the experiment.

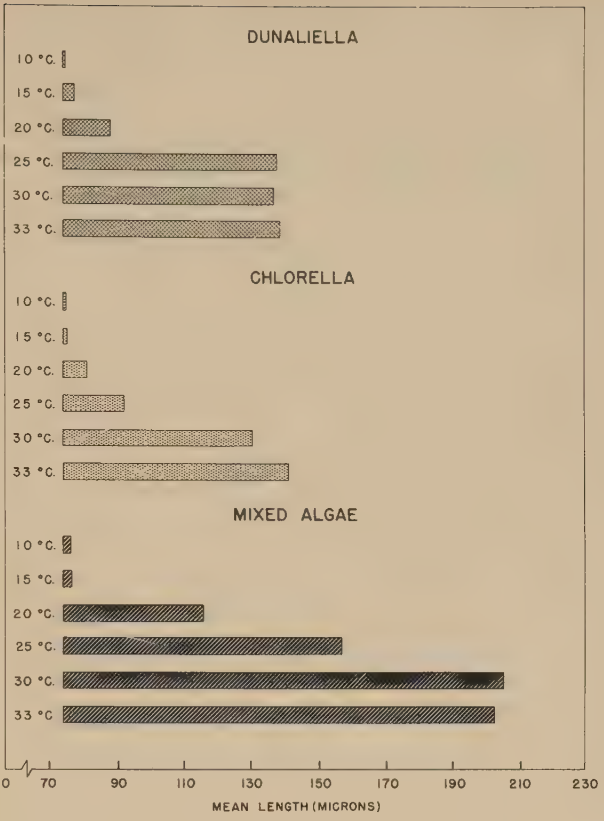

FIGURE 1.—Growth of oyster larvae receiving different foods and reared at different temperatures. Plots are based on mean length of 100 larvae from each temperature at each measuring period.

Since Loosanoff, Miller, and Smith (1951) studied the effect of temperature on the growth rate of clam larvae, we conducted only a single experiment on the effect of different foods on growth of these larvae at different temperatures. Only the *Chlorella* sp. (580) and the mixed algae were tested as foods.

As with oyster larvae, there was a pronounced difference in the ability of clam larvae to utilize the two foods at low temperatures (fig. 3). Although larvae kept at 10.0° C. ingested food, they did not grow and their digestive glands had no

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[1] *Chlorella* sp. (Indiana U. collection #580).

[2] *Dicrateria* sp. (Plymouth collection BII).

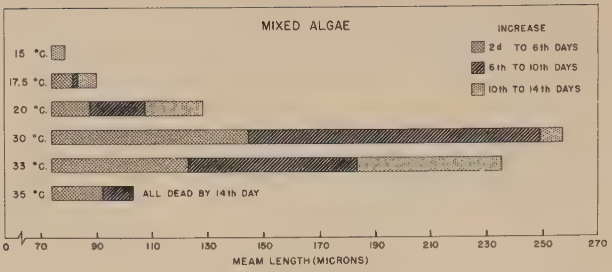

Figure 2.—Growth of oyster larvae receiving the mixture of algae as food and reared at high and low temperatures. Plots based on mean length of 100 larvae from each of duplicate cultures at each temperature at each measuring period. Many of the larvae kept at 30.0° and 33.0° C. set between the 10th and 14th days and were not included in the 14-day samples.

coloration, indicating their inability to digest either food. Larvae receiving *Chlorella* sp. (580) and kept at 15.0° C. likewise did not grow and showed no evidence of digesting this food. The digestive glands of larvae kept at 15.0° C. but receiving mixed algae as food did grow, and their digestive glands had normal color, indicating that some of the species of food organisms added were being digested.

All larvae kept at 20.0° C. grew and showed coloration of the digestive gland. Those receiving *Chlorella* sp. (580), however, averaged only 125.45 μ in mean length by the 12th day, while the larvae receiving the mixed algae grew to a mean length of 198.47 μ, i.e., they had reached setting size. At 30.0° C., larvae receiving *Chlorella* sp. (580) were only approaching setting size by the 12th day (mean length 170.0 μ), while those receiving mixed algae already had metamorphosed and averaged 241.45 μ in length.

Effects of Different Salinities on Temperature Tolerance of Eggs and Larvae of Clams

Our methods of determining the percentage of bivalve eggs developing into normal straight-hinge larvae are accurate to about ±10 percent. Differences of less than 20 percent in the percentages of eggs developing under different conditions, therefore, are of doubtful significance. At our normal salinity, about 27.0 p.p.t., there was no significant difference in the percentage of clam eggs developing normally within the temperature range from 17.5° to 30.0° C. (table 1). At 32.5° and at 15.0° C., however, the percentage was decreased drastically and at 12.5° C. very few normal clam larvae developed.

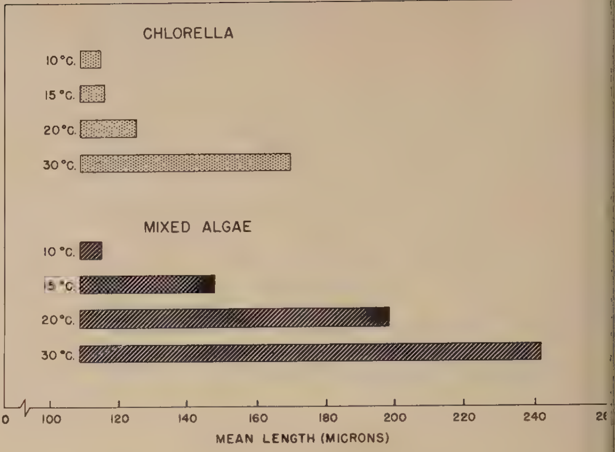

Figure 3.—Growth of clam larvae receiving different foods and reared at different temperatures. Plots are based on mean length of 50 larvae from each of duplicate cultures at each temperature. In cultures fed the mixture of algae and grown at 30.0° C. many larvae had already set by the end of the 10-day experimental period but were included in the samples.

At each temperature, fewer eggs developed normally at a salinity of 22.5 p.p.t. than at 27.0± p.p.t. Temperatures from 22.5° to 25.0° C. appear to be optimum at the salinity of 22.5 p.p.t. Few of the eggs kept at 32.5° or at 15.0° C. developed normally at this salinity. Moreover, 22.5 p.p.t. was the lowest salinity at which any appreciable number of clam eggs developed.

At 20.0 p.p.t. none of the eggs developed into normal larvae at any temperature except in one experiment where a few normal larvae were found at 20.0° and 25.0° C. It should be emphasized, however, that clam larvae can survive at far lower

Table 1.—*Percentage of clam eggs developing to the straight-hinge stage at different combinations of temperature and salinity, Milford, Conn.*[1]

Salinity (P.P.T.)	Temperature (° C.)								
	32.5	30.0	27.5	25.0	22.5	20.0	17.5	15.0	12.5
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
27.0±	39	81	93	95	92	95	94	24	0
22.5	<1	36	65	79	73	56	52	1	<1
20.0	0	0	0	5	0	<1	0	0	0
17.5	0	0	0	0	0	0	0	0	0
15.0	0	0	0	0	0	0	0	0	0
12.5	0	0	0	0	0	0	0	0	0

[1] Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The highest number of eggs developing at any combination of temperature and salinity in each experiment was considered 100 percent for that experiment. Only at temperatures and salinities above the broken line was development of eggs comparatively normal.

salinities than the minimum salinity at which clam eggs can develop. From 20.0° to 30.0° C., survival of clam larvae does not decrease significantly until the salinity falls below 17.5 p.p.t. (table 2). Even at 15.0 p.p.t. approximately 50 percent of the larvae kept at temperatures from 17.5° to 25.0° C. survived.

The decrease in survival of clam larvae with a decrease in salinity was most drastic at high temperatures. At 32.5° C., less than 1 percent survived at a salinity of 17.5 p.p.t. At temperatures of 30.0° and 27.5° C., survival dropped from 75 percent at 17.5 p.p.t. to 25 percent or less at 15.0 p.p.t. In contrast, survival of clam larvae, at 12.5° C., although only 56 percent at our normal salinity of 27.0± p.p.t., still averaged 39 percent after 10 days at a salinity of 12.5 p.p.t.

The growth rate of clam larvae was most rapid at 30.0° C. and at a salinity of 27.0± p.p.t. (table 3). In fact 30.0° C. appeared the best temperature for growth of larvae at salinities of both 27.0± and 22.5 p.p.t., although, at all salinities above 17.5 p.p.t., the growth rate was similar at 30.0°, 27.5° and 25.0° C. A temperature of 32.5° C. was obviously above optimum at all salinities.

The temperature range for satisfactory growth of clam larvae narrowed as the salinity decreased. At 27.0± p.p.t. growth was satisfactory, i.e., at least some larvae approached setting size by the 12th day, at all temperatures from 15.0° to 32.5° C. At 17.5 p.p.t., however, satisfactory growth was limited to the temperature range from 20.0° to 30.0° C.; at 15.0 p.p.t., except at 25.0° C., there was no significant growth of larvae.

Table 2.—*Percentage of clam larvae surviving after 10 days, at different combinations of temperature and salinity, Milford, Conn.*[1]

Salinity (P.P.T.)	Temperature (° C.)								
	32.5	30.0	27.5	25.0	22.5	20.0	17.5	15.0	12.5
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
27.0±	77	83	81	75	87	75	71	61	56
22.5	48	84	87	83	88	76	70	56	46
20.0	16	72	84	76	77	78	62	50	40
17.5	<1	76	74	83	85	69	45	50	49
15.0	0	25	22	57	53	43	58	36	47
12.5	0	<1	0	12	0	9	12	19	39

[1] Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The highest number of larvae surviving at any combination of temperature and salinity in each experiment was considered 100 percent for that experiment. The broken line indicates the ranges of temperature and salinity at which the largest percentage of larvae survived and shows the significant decrease in survival below 17.5 p.p.t.

Table 3.—*Percentage increase in mean length of clam larvae kept at different combinations of temperature and salinity for 10 days, Milford, Conn.*[1]

Salinity (P.P.T.)	Temperature (° C.)								
	32.5	30.0	27.5	25.0	22.5	20.0	17.5	15.0	12.5
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
27.0±	65	98	83	93	83	71	53	30	16
22.5	61	91	85	88	83	68	48	25	12
20.0	54	85	87	82	80	60	39	17	5
17.5	15	63	68	66	59	36	21	5	<1
15.0	0	12	17	31	20	9	3	<1	0
12.5	0	0	0	2	0	0	0	0	0

[1] Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The mean increase in length of larvae in the most rapidly growing set of duplicate cultures in each experiment was considered 100 percent for that experiment. The combinations of salinity and temperature above the broken line were the combinations at which the larvae had the most satisfactory growth and shows the similarity of the growth rates at these combinations.

When clam larvae kept in various salinities at 12.5° C. were transferred to 24.0° C. water of normal salinity (27.0± p.p.t.), those previously in salinities of 17.5 p.p.t. or higher began to grow normally. Larvae previously kept at 12.5° C. in salinities below 17.5 p.p.t., however, did not recover after the transfer to the higher temperature and salinity and all died within 6 days.

Effects of Different Salinities on Temperature Tolerance of Eggs and Larvae of Oysters

In some experiments oyster eggs developed normally at salinities from 20.0 p.p.t. to 27.0± p.p.t. and temperatures from 17.5° to 32.5° C. In other experiments, however, far fewer normal larvae developed from eggs incubated at the marginal temperatures of 32.5° and 17.5° C. This tendency for poor development at the extremes of the above temperature range became even more pronounced when the eggs were incubated at a salinity of 17.5 p.p.t. (table 4). Of the eggs kept in a salinity of 15.0 p.p.t. only in the cultures kept at 27.5° C. did 30 percent or more of the eggs develop, and at 12.5 p.p.t. only an occasional normal larva developed at any temperature. As shown by Davis (1958), the minimum salinity at which oyster eggs will develop normally is determined in part by the salinity at which the parent oysters were kept prior to spawning.

The survival values for oyster larvae (table 5) indicate that satisfactory survival rates (70 percent

TABLE 4.—*Percentage of oyster eggs developing to the straight-hinge stage at different combinations of temperature and salinity, Milford, Conn.*[1]

Salinity (P.P.T.)	Temperature (° C.)					
	32.5	30.0	27.5	22.5	20.0	17.5
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
27.0±	58	86	91	84	83	67
25.0	60	78	88	86	84	80
22.5	58	84	82	88	87	84
20.0	58	77	81	90	86	58
17.5	29	69	89	81	57	10
15.0	1	17	39	24	2	0
12.5	0	0	0	0	0	0
10.0	0	0	0	0	0	0
7.5	0	0	0	0	0	0

[1] Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The highest number of eggs developing at any combination of temperature and salinity in each experiment was considered 100 percent for that experiment. Only at the combinations above the broken line was development comparatively normal.

or better) were limited to temperatures of 27.5° to 32.5° C. and salinities of 10.0 to 27.5 p.p.t. Survival at 22.5° C. was slightly less. Moreover, almost 50 percent of the larvae survived at all salinities and temperatures tested, except that only 23 percent survived in a salinity of 7.5 p.p.t. at 32.5° C., and 22 percent in a salinity of 27.0± p.p.t. at 17.5° C.

As indicated by the percentage increase in mean length at 10 days (table 6), the growth rate of oyster larvae, at all salinities, shows a very sharp break between 27.5° and 22.5° C. Except at temperatures above 22.5° C. and salinities above 12.5 p.p.t., a larval growth rate equivalent to 70 percent of the maximum rate was achieved only in a salinity of 12.5 p.p.t. and temperature of 30.0° C. At salinities of 10.0 p.p.t. or lower, the growth rate was less than 50 percent at all temperatures; at temperatures of 22.5 ° C. or lower the growth rate was less than 50 percent at all salinities.

TABLE 5.—*Percentage of oyster larvae surviving after 8 days at different combinations of temperature and salinity, Milford, Conn.*[1]

Salinity (P.P.T.)	Temperature (° C.)					
	32.5	30.0	27.5	22.5	20.0	17.5
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
27.0±	75	70	76	56	49	22
25.0	68	64	71	54	43	45
22.5	71	66	68	54	45	42
20.0	75	58	66	60	48	37
17.5	78	71	83	65	37	53
15.0	81	74	81	71	67	42
12.5	86	90	73	67	41	40
10.0	67	79	71	66	49	49
7.5	23	38	48	54	53	38

[1] Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The highest number of larvae surviving at any combination of temperature and salinity in each experiment was considered 100 percent for that experiment. Only at the combinations above the broken line was survival of larvae over 70 percent.

TABLE 6.—*Percentage increase in mean length of oyster larvae kept at different combinations of temperature and salinity for 8 days, Milford, Conn.*[1]

Salinity (P.P.T.)	Temperature (° C.)					
	32.5	30.0	27.5	22.5	20.0	17.5
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percen*
27.0±	89	92	76	35	19	9
25.0	84	87	74	32	21	11
22.5	88	91	76	32	21	13
20.0	90	94	76	31	22	12
17.5	85	92	77	31	19	10
15.0	79	87	67	28	18	8
12.5	49	69	52	21	11	4
10.0	30	36	36	14	6	1
7.5	2	11	19	6	2	<1

[1] Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The mean increase in length of larvae in the most rapidly growing set of duplicate cultures in each experiment was considered 100 percent for that experiment. The broken line shows the ranges of temperature and salinity at which the larval growth rate was 70 percent or better.

To determine the time required for larvae to reach metamorphosis at different temperatures, oyster larvae were reared at 20.0°, 22.5°, 25.0°, 27.5°, 30.0° and 32.5° C. and at our normal salinity of 27.0± p.p.t. The experiment continued until all larvae set. The results are shown in table 7.

Because of the slow growth of larvae at low temperatures and low salinities, we did not rear larvae to metamorphosis at all combinations of temperature and salinity.

TABLE 7.—*Number of days for oyster larvae to reach metamorphosis at combinations of different temperatures and 27.0± p.p.t. salinity, Milford, Conn.*

Temperature	Days after fertilization to—	
	Beginning of setting	End of setting
° C.		
30.–32.5	10–12	18–20
27.5	14–16	28–30
25.0	24–26	38–40
22.5	28–30	44–46
20.0	36–40	64–68

To determine (1) the minimum temperature at which oyster larvae, grown to setting size at temperatures of 27.0±1.0° C., could set; and (2) the effect of lowered temperatures on intensity of setting, we conducted five experiments. In each 1-liter beaker, we placed approximately 2,000 oyster larvae reared to 80-mesh size (250–300 μ in length) at a temperature of 27.0°±1.0° C.; two of these cultures were kept at each temperature. Two clean oyster shells in each culture, were examined every second day to determine the occurrence and relative intensity of setting. We counted only those spat occurring on the white inner surface of the test shells. The average numbers of spat per culture recorded are shown in table 8.

In the third experiment, the larvae initially were smaller than in the other experiments, and, although none set at 15.0° or 12.5° C., some still lived 20 days after transfer to these temperatures. It appeared, from these experiments, that at temperatures of 15.0° and 12.5° C. the only larvae that set were those that were mature and ready to set at the time of transfer to these temperatures. Smaller immature larvae, although living more than 20 days after transfer, apparently were unable to develop to the setting stage.

At temperatures from 25.0° to 17.5° C., the number of larvae completing metamorphosis declined with each decrease in temperature, and the time required for setting increased. The decrease in intensity of setting with decreasing temperature within this range is probably the result of the cumulative mortality of larvae as a result of the slower growth rate and consequent lengthening of the larval period.

TABLE 8.—*Average numbers of spat at combinations of different temperatures and 27.0± p.p.t. salinity, Milford, Conn.*[1]

Temperature	Average spat per culture				
	1st experiment	2d experiment	3d experiment	4th experiment	5th experiment
° C.	*Number*	*Number*	*Number*	*Number*	*Number*
25.0	293	----------	723	920	604
22.5	181	723	----------	----------	----------
20.0	170	519	----------	----------	----------
17.5	----------	397	----------	----------	----------
15.0	----------	----------	0	67	----------
12.5	----------	----------	0	33	1
10.0	----------	----------	----------	----------	0

[1] Oyster larvae used in the individual experiments were grown to setting size at temperatures of 27.0±1.0° C. and a normal salinity of 27.0±p.p.t.

DISCUSSION

The failure of bivalve larvae to grow at low temperatures appears to be the result of their inability to digest available food. Our experiments demonstrated that larvae survived for long periods and ingested food at temperatures below the minimum temperature at which they grow. Moreover, since larvae can utilize some foods at lower temperatures than other foods (figs. 1 and 3), perhaps the enzyme systems needed to digest algae without cell walls, such as the chrysomonads, are active at lower temperatures than are the enzyme systems required to digest algae that have cell walls, such as *Chlorella*. The increase, with increase in temperature, in growth rate of larvae fed any one food probably results from increased activity of the enzyme system at higher temperatures.

From our knowledge of the temperature and salinity tolerances of the food organisms used in these experiments, there is no reason to suspect that the reduced growth rate of larvae at low temperatures and salinities results from an indirect effect on the food organisms. Ukeles (1961), however, showed that at temperatures of 27.0° C. or higher the cells of *I. galbana* and *M. lutheri* are destroyed, while cells of *Chlorella* sp. (580) survive even at 33.0° C.

The growth rate of oyster larvae receiving *Chlorella* continued to increase with each increase in temperature up to 33.0° C., while larvae fed the mixture of algae showed no increase between 30.0° and 33.0° C. (fig. 1). It seems probable that in the latter case any increase in activity of the enzyme systems of the larvae at 33.0° C. was offset by a reduction in the amount of food available due to the destruction of cells of *I. galbana* and *M. lutheri*. We believe, therefore, that our results at higher temperatures may be partly due to an indirect effect on the larvae through the food chain. Nevertheless, the drastic reduction in rate of growth at 35.0° C. and the heavy mortality of larvae (fig. 2) almost certainly reflect a direct effect of temperature on the larvae themselves.

Both clam and oyster larvae survived in fair numbers and grew appreciably in salinities significantly lower than the minimum salinity at which eggs develop normally. There are, however, striking differences in the tolerances of the larvae of these two species of lamellibranchs. Virtually none of the clam eggs kept at 12.5° C., the minimum temperature at which clam larvae will grow, developed normally (table 1). In contrast, an approximately normal number of oyster eggs developed at 17.5° C. (table 4), which is the lowest temperature at which oyster larvae show appreciable growth.

The most notable interspecific differences were to the effects of temperature and salinity on growth of larvae. Growth of clam larvae was comparatively little affected by temperature differences within the range from 20.0° to 30.0° C., whereas growth of oyster larvae was markedly affected by every increase in temperature from 17.5° to 30.0° C. The optimum temperature for growth of clam larvae was not well defined but appeared to drop from 30.0° C. at salinities of 22.5 p.p.t. and higher to 27.5° C. at salinities of 17.5 and 20.0 p.p.t. and to 25.0° C. at a salinity of 15.0 p.p.t. Differences in the growth rate of clam larvae at temperatures from 22.5° to 30.0° C. appeared to be almost random, and the optimum growth rate occurred at temperatures other than 30.0° C. at each salinity tested in one or more experiments (table 9).

In contrast, there is a marked stepwise increase in the growth rate of oyster larvae with each increase in temperature up to 30.0° C. (table 6). There is a fairly well defined optimum between 30.0° and 32.5° C. for all salinities except 7.5 p.p.t. where the optimum is 27.5° C. Differences between the growth rate of oyster larvae at 30.0° and at 32.5° C. were usually small with sometimes one and sometimes the other temperature giving the maximum growth rate, indicating that the optimum might well lie between these two temperatures.

Clam and oyster larvae differed also in their growth response to different salinity levels, but whereas oyster larvae were more sensitive than clam larvae to differences in temperature, the latter appeared more sensitive to salinity differences. Growth of clam larvae, at almost all temperatures, decreased stepwise with each decrease in salinity (table 3), and the maximum salinity (27.0± p.p.t.) was the most nearly optimum of the salinities tested. The growth rate of oyster larvae, however, was relatively constant at each temperature within the salinity range from 15.0 to 27.5 p.p.t. and there was no apparent optimum salinity (table 6).

Kinne and Kinne (1962) stated that extreme conditions of temperature, salinity, and oxygen could induce developmental arrest, and that "such arrest may remain reversible if conditions are normalized within hours or a few days; longer periods cause irreversible damage; they are lethal." In our experiments the "developmental arrest" of clam larvae kept at 12.5° C. and at salinities above 17.5 p.p.t. was reversible, but irreversible at salinities of 15.0 p.p.t. or lower.

The data on clam eggs and larvae were remarkably consistent, i.e., there were no major differences between successive experiments in the percentage of eggs developing to the straight-hinge larval stage, in the survival of larvae or in the growth rate of larvae (tables 9 and 10). In experiments with oyster eggs and larvae, however, there were large differences between experiments on the effect of salinity. Moreover, while the data on the salinity tolerances of clam eggs and larvae agreed quite well with Davis (1958), the data on salinity tolerances of eggs and larvae of oysters did not.

In the first experiment with oyster eggs and larvae, for example, the optimum salinity for growth of oyster larvae at all temperatures was either 25.0 or 27.0±p.p.t. (exp. 1, table 11). In experiments 2 and 3, however, the optimum salinity at most temperatures was between 15.0 and 20.0 p.p.t. Because we suspected that better growth at lowered salinities might be a result of diluting toxic external metabolites of algal blooms that sometimes occur in Milford Harbor (Davis and Chanley, 1955), in the fourth experiment we used sea water collected from a considerable distance offshore in Long Island Sound. The egg development data from this experiment (exp. 4, table 12) showed unexpectedly that dilution of dissolved toxins in sea water may indeed be responsible for better results in lowered salinities. None of the eggs kept in the undiluted offshore sea water developed into normal larvae, indicating that our offshore sea water contained a considerable amount of toxins. Although an approximately normal percentage of straight-hinge larvae developed at some temperatures in 20.0 p.p.t., a normal percentage did not occur at all temperatures except in cultures where this sea water had been diluted to a salinity of 17.5 p.p.t. or lower.

In experiments 5 and 7 (tables 11 and 12),

TABLE 9.—*Growth of clam larvae at 12 days, at different combinations of salinity and temperature, Milford, Conn.*

[Data from individual experiments using clam eggs and larvae]

Salinity (p.p.t.) and temperature (° C)	Mean length of larvae at 12 days					Increase in mean length of larvae (2d to 12th days)				
	Experiment				Average	Experiment				Average
	1	2	3	4		1	2	3	4	
27.5 p.p.t.:	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
12.5°			123.8	126.4	125.1			16.0	15.2	15.6
15.0°			141.7	142.4	142.1			31.3	27.7	29.5
17.5°			172.5	168.0	170.3			57.6	47.8	52.7
20.0°	188.9	193.4	188.8	195.2	191.5	63.9	78.4	71.5	69.1	70.7
22.5°	213.9	198.4			206.2	84.3	83.1			82.7
25.0°	213.1	203.6	222.2	234.7	218.4	83.7	88.0	100.0	100.0	92.9
27.5°	211.3	200.0			205.7	82.2	84.6			83.4
30.0°	233.3	216.4	218.2	230.9	224.9	100.0	100.0	96.6	97.0	98.4
32.5°	188.0	181.2			184.6	63.3	67.0			65.1
22.5 p.p.t.:										
12.5°			120.9	121.0	121.0			13.6	11.0	12.3
15.0°			135.7	137.5	136.6			26.1	23.9	25.0
17.5°			164.3	164.3	164.3			50.6	44.9	47.7
20.0°	190.6	192.5	184.9	185.5	188.4	65.5	77.6	68.2	61.5	68.2
22.5°	207.2	201.7			204.5	78.9	86.2			82.5
25.0°	211.6	202.1	212.2	223.7	212.8	82.4	86.6	91.5	91.4	88.0
27.5°	212.3	203.3			207.8	83.0	87.7			85.3
30.0°	216.7	198.9	215.0	233.1	215.9	86.9	83.6	93.9	98.7	90.8
32.5°	177.4	182.0			179.7	54.8	67.8			61.3
20 p.p.t.:										
12.5°			110.7	112.7	111.7			4.9	4.5	4.7
15.0°			124.5	129.8	127.2			16.6	17.9	17.3
17.5°			152.3	154.9	153.6			40.4	37.5	39.0
20.0°	181.3	184.6	172.6	177.3	179.0	58.0	70.2	57.7	55.1	60.2
22.5°	199.5	203.9			201.6	72.6	88.3			80.4
25.0°	206.0	204.3	203.1	210.4	205.9	77.9	88.6	83.7	81.0	82.3
27.5°	217.9	200.8			209.4	87.6	85.4			86.5
30.0°	212.8	207.5	198.2	218.1	209.2	83.4	91.8	79.5	87.0	85.4
32.5°	169.0	173.9			171.4	48.0	60.2			54.1
17.5 p.p.t.:										
12.5°			105.9	106.1	106.0			.8	.0	.4
15.0°			111.6	112.9	112.3			5.6	4.6	5.1
17.5°			132.6	131.7	132.2			23.5	19.3	21.4
20.0°	157.2	150.9	145.8	148.0	150.5	38.5	39.0	34.8	32.1	36.1
22.5°	184.4	170.8			177.6	60.5	57.6			59.1
25.0°	193.4	188.5	179.1	182.1	185.8	67.7	73.9	63.2	58.8	65.9
27.5°	188.2	186.6			187.4	63.5	72.1			67.8
30.0°	184.6	187.0	175.7	183.1	182.6	60.6	72.4	60.3	59.6	63.2
32.5°	.0	141.3			[1] 141.3	.0	29.6			14.8
15.0 p.p.t.:										
12.5°			104.2	104.0	104.1			.0	.0	.0
15.0°			106.3	106.9	106.6			1.1	.0	.6
17.5°			110.1	110.0	110.1			4.4	2.3	3.4
20.0°	120.9	121.4	116.0	116.5	118.7	9.1	11.0	9.4	7.4	9.2
22.5°	138.2	127.1			132.6	23.1	16.3			19.7
25.0°	153.1	142.9	140.7	139.2	179.2	35.2	31.1	30.5	25.2	30.5
27.5°	152.7	.0			[1] 152.7	34.8	.0			17.4
30.0°	125.9	.0	129.3	124.3	126.5	13.2	.0	20.7	13.5	11.9
32.5°	.0	.0			.0	.0	.0			.0
12.5 p.p.t.:										
12.5°			104.1	104.9	104.5			.0	.0	.0
15.0°			102.7	104.2	103.5			.0	.0	.0
17.5°			103.7	101.5	102.6			.0	.0	.0
20.0°	.0	.0	103.5	104.1	103.8	.0	.0	.0	.0	.0
22.5°	.0	.0			.0	.0	.0			.0
25.0°	111.7	.0	112.8	103.3	109.3	1.7	.0	6.7	.0	2.1
27.5°	.0	.0			.0	.0	.0			.0
30.0°	.0	.0	102.8	.0	[1] 102.8	.0	.0	.0	.0	.0
32.5°	.0	.0			.0	.0	.0			.0

[1] All died in one experiment. Average of single experiment in which some survived.

oyster larvae kept at 27.5° and 30.0° C. and salinities of 7.5 and 10.0 p.p.t. showed a much better rate of survival and growth than in experiment 6 of this series or recorded by Davis (1958). It is possible that in experiments 5 and 7 we happened to get genetic crosses that were better adapted to tolerate low salinities than the general population of Long Island Sound oysters. It is conceivable that the variations in growth noted in experiments 1, 2 and 3 also were genetic and that the Long Island Sound oyster population is heterogeneous in tolerance to salinity.

Regardless of the possible effect of toxic pollutants and of genetic factors, the general features of the effect of lowered salinities on temperature tolerance appear clear. By every measure of temperature tolerance, the tolerated range of temperatures narrowed as the salinity decreased. As measured by the percentage of eggs developing normally and as measured by the growth of larvae, this narrowing of the range resulted from more rapid decreases at both extremes of the temperature range than at intermediate temperatures. As measured by the survival of clam larvae, the

TABLE 10.—*Development of clam eggs to straight-hinge larval stage and survival of clam larvae at 12 days, at different combinations of salinity and temperature, Milford, Conn.*

[Data from individual experiments using clam eggs and larvae]

Salinity (p.p.t.) and temperature (°C)	Eggs developing to straight-hinge larval stage					Larvae surviving to 12th day				
	Experiment				Average	Experiment				Average
	1	2	3	4		1	2	3	4	
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
27.5 p.p.t.:										
12.5°			0.0	0 0	0.0			31.8	79.6	55.7
15.0°			1.7	56.0	23.6			56.8	65.3	61.0
17.5°			100.0	88.1	94.1			63.6	78.2	70.9
20.0°	99.4	93.4	88.1	98.8	94.9	73.9	85.0	71.2	69.4	74.9
22.5°	92.9	90.1			91.5	74.8	100.0			87.4
25.0°	100.0	93.4	85.6	100.0	94.8	86.6	87.6	62.7	64.6	75.4
27.5°	86.5	100.0			93.3	79.9	83.3			81.4
30.0°	80.0	79.3	80.5	82.7	80.6	89.8	78.2	64.4	100.0	83.1
32.5°	78.1	.0			39.0	61.1	92.3			76.7
22.5 p.p.t.:										
12.5°			.0	1.8	.9			32.2	59.9	46.0
15.0°			1.7	0.6	1.1			34.7	78.2	56.4
17.5°			53.4	50.6	52.0			49.2	89.8	69.5
20.0°	58.7	49.6	62.7	50.6	55.4	91.9	82.5	50.8	78.9	76.0
22.5°	80.0	66.1			73.1	85.5	90.2			87.9
25.0°	80.6	60.3	94.1	79.8	78.7	91.2	88.9	60.2	93.2	83.4
27.5°	70.3	61.2			65.8	89.4	85.5			87.4
30.0°	32.9	6.6	39.8	63.1	35.6	92.6	80.3	76.3	87.1	84.1
32.5°	.0	.8			.4	55.8	39.3			47.6
20. p.p.t.:										
12.5°			.0	.0	.0			14.4	66.0	40.2
15.0°			.0	.0	.0			33.1	66.7	49.9
17.5°			.0	.0	.0			37.3	86.4	61.9
20.0°	.0	.0	.0	1.8	.5	82.0	86.8	51.7	91.8	78.1
22.5°	.0	.0			.0	86.9	66.7			76.8
25.0°	.0	.0	.8	19.6	5.1	99.3	88.5	44.9	72.8	76.4
27.5°	.0	.0			.0	86.9	82.1			84.5
30.0°	.0	.0	.0	.0	.0	89.4	42.7	66.9	89.1	72.0
32.5°	.0	.0			.0	6.0	25.2			15.6
17.5 p.p.t.:										
12.5°			.0	.0	.0			45.8	51.7	48.8
15.0°			.0	.0	.0			39.0	61.2	50.1
17.5°			.0	.0	.0			37.3	61.2	44.6
20.0°	.0	.0	.0	.0	.0	95.8	71.4	33.9	74.1	68.8
22.5°	.0	.0			.0	86.6	82.5			84.5
25.0°	.0	.0	.0	.0	.0	100.0	84.2	67.8	80.3	83.1
27.5°	.0	.0			.0	89.8	57.3			73.5
30.0°	.0	.0	.0	.0	.0	63.3	54.3	100.0	86.4	76.0
32.5°	.0	.0			.0	.0	.9			.5
15.0 p.p.t.:										
12.5°			.0	.0	.0			75.4	18.4	46.9
15.0°			.0	.0	.0			55.1	17.0	36.1
17.5°			.0	.0	0			78.0	37.4	57.7
20.0°	.0	.0	.0	.0	.0	35.3	17.5	82.2	36.1	42.8
22.5°	.0	.0			.0	76.7	28.6			52.7
25.0°	.0	.0	.0	.0	.0	62.9	22.6	92.4	51.7	57.4
27.5°	.0	.0			.0	43.5	.0			21.8
30.0°	.0	.0	.0	.0	.0	3.9	.0	63.6	32.7	25.1
32.5°	.0	.0			.0	.0	.0			.0
12.5 p.p.t.:										
12.5°			.0	.0	.0			63.6	14.3	38.9
15.0°			.0	.0	.0			30.0	8.8	19.4
17.5°			.0	.0	.0			19.5	3.4	11.5
20.0°	.0	.0	.0	.0	.0	.0	.0	24.6	9.5	8.5
22.5°	.0	.0			.0	.0	.0			.0
25.0°	.0	.0	.0	.0	.0	.7	.0	44.1	3.4	12.1
27.5°	.0	.0			.0	.0	.0			.0
30.0°	.0	.0	.0	.0	.0	.0	.0	1.7	.0	.4
32.5°	.0	.0			.0	.0	.0			.0

narrowing of the range was primarily by marked decreases in percent survival at the higher temperatures. With oyster larvae, in these experiments, apparently at even the lowest salinity tested (7.5 p.p.t.) we were just beginning to get marked effects of salinity on survival. It would appear that here, also, the narrowing of the range would be primarily by heavy mortality at the higher temperatures if the salinity were to be lowered still further.

The difference in the temperature requirements for satisfactory growth of clam and oyster larvae probably accounts for some of the difference in success of recruitment of these two species of bivalves in many shellfish-producing areas. While many clam larvae, in water at proper salinity, reached setting size by the 12th day at only 15.0° C., oyster larvae in 20.0° C. water required 36 to 40 days to begin setting. Although the actual time required in natural waters would be altered by the type and quantity of food and by other factors, the relative time required probably

TABLE 11.—*Growth of oyster larvae at 10 days, at different combinations of salinity and temperature, Milford, Conn.*

[Data from individual experiments using oyster eggs and larvae]

Salinity (p.p.t.) and temperature (° C)	Mean length of larvae at 10 days								Increase in mean length of larvae (2d to 10th days)							
	Experiment							Average	Experiment							Average
	1	2	3	4	5	6	7		1	2	3	4	5	6	7	
27.5 p.p.t.:	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
17.5°	94.70	81.20	82.65	83.07	-----	83.34	87.53	85.42	22.2	6.7	4.9	4.2	-----	7.0	8.5	8.7
20.0°	112.76	86.76	86.60	102.85	-----	92.23	106.46	97.93	41.8	12.7	7.5	14.5	-----	15.4	19.8	18.9
22.5°	130.94	99.74	102.50	141.21	-----	116.15	130.37	120.15	63.1	26.7	17.8	34.4	-----	34.7	34.1	35.1
27.5°	161.05	121.32	185.94	224.38	-----	170.45	208.23	178.59	97.1	49.9	71.8	77.6	-----	80.4	80.7	76.3
30.0°	163.59	142.46	223.75	242.26	-----	190.17	240.50	200.35	100.0	72.7	96.3	86.8	-----	97.0	100.0	92.1
32.5°	152.73	138.86	229.45	243.77	-----	193.75	220.00	196.33	87.9	68.8	100.0	87.6	-----	100.0	87.7	88.9
25.0 p.p.t.:																
17.5°	99.50	79.44	83.98	88.56	-----	-----	-----	87.87	27.1	4.8	5.8	7.0	-----	-----	-----	11.2
20.0°	107.83	91.33	89.48	107.25	-----	-----	-----	98.97	37.1	17.6	9.4	19.3	-----	-----	-----	20.9
22.5°	120.83	103.97	105.15	141.73	-----	-----	-----	117.92	51.7	31.2	11.1	34.6	-----	-----	-----	32.2
27.5°	150.65	130.37	185.88	229.00	-----	-----	-----	173.95	85.8	59.7	71.8	80.0	-----	-----	-----	74.3
30.0°	150.98	139.71	224.55	251.44	-----	-----	-----	192.75	91.4	69.8	96.9	91.6	-----	-----	-----	86.6
32.5°	156.00	140.98	226.25	239.99	-----	-----	-----	191.87	82.5	71.1	97.7	85.7	-----	-----	-----	84.3
22.5 p.p.t.:																
17.5°	97.99	86.96	82.88	91.99	-----	-----	-----	89.96	26.0	12.9	5.1	8.8	-----	-----	-----	13.2
20.0°	108.02	93.36	90.20	110.00	-----	-----	-----	100.39	37.3	19.8	10.2	18.2	-----	-----	-----	21.4
22.5°	114.84	103.57	101.68	144.02	-----	-----	-----	116.03	45.0	30.8	17.3	35.8	-----	-----	-----	32.2
27.5°	157.36	137.85	164.98	238.27	-----	-----	-----	174.62	93.0	67.2	58.3	84.8	-----	-----	-----	75.8
30.0°	160.29	156.25	213.18	256.61	-----	-----	-----	194.58	96.3	83.3	89.5	94.3	-----	-----	-----	90.9
32.5°	152.63	149.97	226.90	240.40	-----	-----	-----	193.48	87.6	80.8	98.4	85.9	-----	-----	-----	88.2
20.0 p.p.t.:																
17.5°	94.47	85.49	85.00	90.09	-----	-----	-----	88.76	22.0	11.3	6.5	7.8	-----	-----	-----	11.9
20.0°	107.97	92.59	95.60	110.32	-----	-----	-----	101.62	37.2	19.0	13.3	18.3	-----	-----	-----	22.0
22.5°	113.60	98.74	109.23	137.96	-----	-----	-----	114.88	43.6	25.6	22.2	32.7	-----	-----	-----	31.0
27.5°	139.83	136.62	191.13	244.42	-----	-----	-----	178.00	73.2	66.4	75.2	88.0	-----	-----	-----	75.7
30.0°	153.80	156.25	230.80	267.62	-----	-----	-----	202.12	88.9	87.6	100.0	100.0	-----	-----	-----	94.1
32.5°	150.25	160.23	220.85	243.40	-----	-----	-----	193.68	85.0	91.9	94.4	88.0	-----	-----	-----	89.8
17.5 p.p.t.:																
17.5°	93.93	85.83	84.55	89.73	-----	79.00	85.81	86.48	20.8	11.7	6.2	7.6	-----	3.4	7.4	9.5
20.0°	100.38	95.05	97.03	112.56	-----	92.79	102.39	100.03	28.6	21.6	14.3	19.5	-----	15.0	17.3	19.4
22.5°	108.43	100.95	111.50	136.87	-----	113.59	124.58	115.99	37.7	28.0	23.6	32.1	-----	32.5	30.6	30.8
27.5°	131.58	147.92	198.18	241.35	-----	166.98	197.12	180.52	63.9	78.6	79.8	86.4	-----	77.5	74.0	76.7
30.0°	143.45	160.47	223.58	265.29	-----	189.30	224.35	201.73	77.3	92.1	96.2	98.8	-----	96.3	90.3	91.8
32.5°	144.53	164.52	217.99	231.93	-----	175.10	204.43	189.75	78.5	93.7	92.6	81.5	-----	84.3	78.4	84.8
15.0 p.p.t.:																
17.5°	89.81	86.26	82.90	85.23	-----	77.96	84.42	84.43	16.7	12.1	5.1	5.3	-----	2.5	6.6	8.1
20.0°	95.28	97.63	94.75	111.40	-----	89.70	102.36	98.52	22.9	24.4	12.8	18.9	-----	12.4	17.3	18.1
22.5°	105.08	101.06	109.95	131.32	-----	104.78	126.20	113.07	34.0	28.1	22.6	29.2	-----	25.1	31.6	28.4
27.5°	120.50	144.20	181.89	243.83	-----	130.59	197.73	169.79	51.4	74.6	69.2	87.7	-----	46.8	74.4	67.4
30.0°	134.50	166.77	212.80	261.52	-----	160.77	235.62	195.33	67.2	99.0	89.2	96.8	-----	72.2	97.1	86.9
32.5°	139.08	167.75	209.59	220.44	-----	153.90	192.52	180.55	72.3	100.0	87.2	75.5	-----	66.4	71.3	78.8
12.5 p.p.t.:																
17.5°	-----	-----	-----	-----	-----	76.20	84.28	80.24	-----	-----	-----	-----	-----	1.0	6.5	3.8
20.0°	-----	-----	-----	-----	-----	86.05	95.69	90.87	-----	-----	-----	-----	-----	9.3	13.3	11.3
22.5°	-----	-----	-----	-----	-----	95.85	114.05	104.95	-----	-----	-----	-----	-----	17.6	24.3	21.0
27.5°	-----	-----	-----	-----	-----	118.47	186.42	152.45	-----	-----	-----	-----	-----	36.6	67.6	52.1
30.0°	-----	-----	-----	-----	-----	142.31	207.60	174.95	-----	-----	-----	-----	-----	56.7	80.3	68.5
32.5°	-----	-----	-----	-----	-----	145.37	138.85	142.11	-----	-----	-----	-----	-----	59.3	39.2	49.3
10.0 p.p.t.:																
17.5°	-----	-----	-----	-----	77.00	74.88	77.99	76.62	-----	-----	-----	-----	-----	.0	2.7	1.4
20.0°	-----	-----	-----	-----	83.80	80.25	86.51	83.52	-----	-----	-----	-----	-----	4.4	7.8	6.1
22.5°	-----	-----	-----	-----	103.40	86.58	103.54	97.84	-----	-----	-----	-----	-----	9.8	18.0	13.5
27.5°	-----	-----	-----	-----	159.50	103.81	151.70	138.37	-----	-----	-----	-----	-----	24.3	46.9	35.6
30.0°	-----	-----	-----	-----	172.70	106.14	150.69	143.18	-----	-----	-----	-----	-----	26.4	46.3	36.3
32.5°	-----	-----	-----	-----	138.40	109.30	124.42	124.04	-----	-----	-----	-----	-----	28.9	30.5	29.7
7.5 p.p.t.:																
17.5°	-----	-----	-----	-----	73.60	72.26	75.26	73.71	-----	-----	-----	-----	-----	.0	1.1	.6
20.0°	-----	-----	-----	-----	76.40	73.95	79.96	76.77	-----	-----	-----	-----	-----	.0	3.9	2.0
22.5°	-----	-----	-----	-----	84.50	75.54	91.10	83.71	-----	-----	-----	-----	-----	.5	10.6	5.6
27.5°	-----	-----	-----	-----	117.40	84.76	123.43	108.53	-----	-----	-----	-----	-----	8.2	29.9	19.1
30.0°	-----	-----	-----	-----	103.00	79.69	103.09	95.26	-----	-----	-----	-----	-----	3.9	17.8	10.9
32.5°	-----	-----	-----	-----	79.40	74.32	79.25	77.66	-----	-----	-----	-----	-----	.0	3.5	1.8

would be comparable. In Long Island Sound, where the temperature rarely gets above 21.0° C. and where there are strong tides, during such a greatly prolonged free-swimming period most oyster larvae might be lost by dispersal and by natural predation and mortality. The more rapidly maturing clam larvae, however, would suffer much less loss from these causes.

The fact that mature oyster larvae reared at relatively high temperature (27.0° C.) could set when transferred to temperatures as low as 12.5° C. suggests that oyster larvae that had grown to setting size in protected shallow estuaries where the temperature reached 25.0° to 30.0° C. might well be the source of mature larvae that set in the colder waters of Long Island Sound and similar areas.

SUMMARY

1. Both clam and oyster larvae can ingest foods at significantly lower temperatures than the minimum temperatures at which they can digest and

TABLE 12.—*Development of oyster eggs to straight-hinge larval stage and survival of oyster larvae at 10 days, at different combinations of salinity and temperature, Milford, Conn.*

[Data from individual experiments using oyster eggs and larvae]

Salinity (p.p.t.) and temperature (° C.)	Eggs developing to straight-hinge larval stage								Larvae surviving to 10th day							
	Experiment							Average	Experiment							Average
	1	2	3	[1] 4	5	6	7		1	2	3	4	5	6	7	
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
27.5 p.p.t.:																
17.5°	90.8	70.3	79.1	0.0	30.5	38.7	90.9	66.7	23	31	81	35	--------	21	38	22
20.0°	97.5	85.0	100.0	.0	77.3	72.4	66.4	83.1	39	35	86	28	--------	39	66	49
22.5°	100.0	88.4	72.8	.0	88.7	51.5	100.0	83.6	46	20	87	52	--------	47	86	56
27.5°	92.5	93.5	76.2	.0	90.8	100.0	94.1	91.2	64	59	100	63	--------	84	84	76
30.0°	83.0	83.7	75.7	.0	88.7	88.3	97.7	86.2	49	60	79	60	--------	100	79	70
32.5°	82.0	71.6	51.9	.0	20.6	20.9	98.2	57.5	65	54	94	60	--------	86	90	75
25.0 p.p.t.:																
17.5°	75.5	87.0	78.1	.0	--------	--------	--------	80.2	26	30	87	37	--------	--------	--------	45
20.0°	87.4	85.5	81.0	.0	--------	--------	--------	83.7	33	31	72	35	--------	--------	--------	43
22.5°	99.2	91.0	67.0	7.6	--------	--------	--------	85.7	40	35	83	56	--------	--------	--------	54
27.5°	75.3	91.0	96.6	32.7	--------	--------	--------	87.6	54	81	94	54	--------	--------	--------	71
30.0°	80.5	75.5	78.6	1.2	--------	--------	--------	78.2	54	64	82	56	--------	--------	--------	64
32.5°	63.5	50.5	67.0	.0	--------	--------	--------	60.3	52	64	86	71	--------	--------	--------	68
22.5 p.p.t.:																
17.5°	67.8	81.5	82.5	5.8	--------	--------	--------	83.9	20	29	83	36	--------	--------	--------	42
20.0°	95.0	85.0	81.1	55.0	--------	--------	--------	87.0	36	22	78	42	--------	--------	--------	45
22.5°	99.2	91.0	81.1	71.9	--------	--------	--------	88.4	50	32	77	56	--------	--------	--------	54
27.5°	93.3	87.6	76.2	.0	--------	--------	--------	82.4	46	88	84	55	--------	--------	--------	68
30.0°	84.0	96.5	71.8	4.1	--------	--------	--------	84.1	43	72	84	66	--------	--------	--------	66
32.5°	62.6	50.6	61.6	.0	--------	--------	--------	58.3	61	75	84	64	--------	--------	--------	71
20.0 p.p.t.:																
17.5°	41.5	67.0	64.6	9.9	--------	--------	--------	57.7	13	47	71	27	--------	--------	--------	37
20.0°	94.2	91.8	72.3	81.3	--------	--------	--------	86.1	24	25	88	53	--------	--------	--------	48
22.5°	95.0	96.5	77.2	84.2	--------	--------	--------	89.6	68	31	73	68	--------	--------	--------	60
27.5°	82.0	97.0	63.1	100.0	--------	--------	--------	80.7	49	63	83	67	--------	--------	--------	66
30.0°	80.5	96.0	54.3	42.7	--------	--------	--------	76.9	51	38	79	62	--------	--------	--------	58
32.5°	51.6	61.4	60.2	10.5	--------	--------	--------	57.7	65	69	97	62	--------	--------	--------	75
17.5 p.p.t.:																
17.5°	.0	12.0	7.8	.0	.0	1.2	46.8	9.7	82	73	49	31	--------	46	38	53
20.0°	63.5	55.4	38.3	60.2	20.6	70.6	88.2	56.7	67	19	61	43	--------	33	57	37
22.5°	95.8	79.0	58.2	84.2	79.4	71.2	95.9	80.5	81	24	78	76	--------	60	72	65
27.5°	89.0	100.0	60.2	91.8	100.0	93.3	85.4	88.5	88	65	80	100	--------	81	85	83
30.0°	86.5	77.4	47.1	28.1	69.5	82.2	92.7	69.1	83	64	81	40	--------	68	90	71
32.5°	29.6	25.3	22.8	4.1	6.4	38.0	74.1	28.6	87	88	73	56	--------	85	81	78
15.0 p.p.t.:																
17.5°	.0	.0	.0	.0	.0	.0	.0	.0	52	57	43	28	--------	29	40	42
20.0°	.8	.0	2.4	.0	.0	.0	7.7	1.6	79	88	80	47	--------	55	50	67
22.5°	28.0	5.3	23.3	18.1	3.5	24.5	63.2	23.7	90	100	73	75	--------	24	65	71
27.5°	34.8	13.3	31.1	29.8	35.5	55.8	73.6	39.1	100	86	80	45	--------	78	97	81
30.0°	6.8	.7	8.7	14.6	8.5	28.8	48.2	16.6	81	91	72	37	--------	71	90	74
32.5°	.0	.0	1.0	1.8	.0	1.2	2.3	.9	81	95	80	70	--------	74	87	81
12.5 p.p.t.:																
17.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	56	23	40
20.0°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	33	49	41
22.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	68	66	67
27.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	63	83	73
30.0°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	79	100	90
32.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	84	87	86
10.0 p.p.t.:																
17.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	49	48	49
20.0°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	74	24	49
22.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	67	65	66
27.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	61	81	71
30.0°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	63	94	79
32.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	65	68	67
7.5 p.p.t.:																
17.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	42	34	38
20.0°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	64	41	53
22.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	57	50	54
27.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	32	64	48
30.0°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	21	54	38
32.5°	--------	--------	--------	--------	.0	.0	.0	.0	--------	--------	--------	--------	--------	39	7	23

[1] Omitted from calculations (see text).

assimilate the food organisms used in these experiments.

2. Both clam and oyster larvae can digest and assimilate naked flagellates, such as *M. lutheri* and *I. galbana*, at lower temperatures than those at which they can utilize algae with cell walls, such as *Chlorella* sp. (580).

3. The minimum temperature for appreciable growth of clam larvae fed naked flagellates was 12.5° C. and the minimum for growth of oyster larvae was 17.5° C.

4. The optimum salinity for growth of clam larvae was 27.0 p.p.t. (the highest salinity tested) or possibly higher.

5. There was no well-defined optimum temperature for growth of clam larvae at any salinity;

maximum growth occurred at temperatures ranging from 25.0° to 30.0° C. in different experiments at almost all salinities.

6. The optimum temperature for growth of oyster larvae was between 30.0° and 32.5° C. in all experiments for all salinities except 7.5 p.p.t. where the optimum was 27.5° C.

7. There was no well-defined optimum salinity for growth of oyster larvae at any temperature; maximum growth occurred in salinities varying from 15.0 to 27.0 p.p.t. in different experiments at some temperatures and from 20.0 to 27.0 p.p.t. even at 17.5° C., where there was least variation.

8. The effect of reduced salinities on larvae of both clams and oysters was to reduce the range of temperatures tolerated. The temperature range for development of eggs and growth of larvae was shortened from both ends, whereas the range for survival of clam larvae was reduced at least primarily by heavy mortality at high temperatures.

9. The time required for oyster larvae to reach the setting stage, under our laboratory conditions, ranged from 10–12 days at 30.0° to 32.5° C. to 36–40 days at 20.0° C.

10. Oyster larvae reared to setting size at about 27.0° C. and transferred to lower temperatures could set at temperatures as low as 12.5° C., but the percentage of such larvae successfully completing metamorphosis decreased progressively with each decrease in temperature.

LITERATURE CITED

Costlow, J. D., C. G. Brookhout, and R. Monroe.
1960. The effect of salinity and temperature on larval development of *Sesarma cinereum* (Bosc.) reared in the laboratory. Biological Bulletin, vol. 18, No. 2, pp. 183–202.

Costlow, J. D., C. G. Brookhout, and R. Monroe.
1962. Salinity-temperature effects on the larval development of the crab, *Panopeus herbstii* Milne-Edwards, reared in the laboratory. Physiological Zoology, vol. 35, No. 1, pp. 79–93.

Davis, H. C.
1958. Survival and growth of clam and oyster larvae at different salinities. Biological Bulletin, vol. 114, No. 3, pp. 296–307.

Davis, H. C., and P. E. Chanley.
1955. Effects of some dissolved substances on bivalve larvae. Proceedings National Shellfisheries Association, vol. 46, pp. 59–74.

Davis, H. C., and R. R. Guillard.
1958. Relative value of ten genera of micro-organisms as food for oyster and clam larvae. U.S. Department of Interior, Fish and Wildlife Service, Fishery Bulletin 136, vol. 58, pp. 293–304.

Kinne, O.
1963. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. Oceanography and Marine Biology, An Annual Review, vol. 1, pp. 301–340.

Kinne, O., and Eva Marie Kinne.
1962. Rates of development in embryos of a cyprinodont fish exposed to different temperature-salinity-oxygen combinations. Canadian Journal of Zoology, vol. 40, pp. 231–253.

Loosanoff, V. L., and H. C. Davis.
1950. Conditioning of *V. mercenaria* for spawning in winter and breeding its larvae in the laboratory. Biological Bulletin, vol. 98, No. 1, pp. 60–65.

Loosanoff, V. L., and H. C. Davis.
1963. Rearing of bivalve mollusks. Advances in Marine Biology, Academic Press, vol. 1, pp. 1–136.

Loosanoff, V. L., W. S. Miller, and P. B. Smith.
1951. Growth and setting of larvae of *Venus mercenaria* in relation to temperature. Journal of Marine Research, vol. 10, No. 1, pp. 59–81.

Medcof, J. C., and A. W. H. Needler.
1941. The influence of temperature and salinity on the condition of oysters (*Ostrea virginica*). Journal of the Fisheries Research Board of Canada, vol. 5, No. 3, pp. 253–257.

Ukeles, R.
1961. The effect of temperature on the growth and survival of several marine algal species. Biological Bulletin, vol. 120, No. 2, pp. 255–264.

A CRITICAL STUDY OF PRIBILOF FUR SEAL POPULATION ESTIMATES

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ABSTRACT

Previously unresolved problems in the populations studies of the Pribilof fur seal are reviewed. The tagging estimates of fur seal pups may have been biased by tag mortality and hence the apparent year class fluctuations after 1952 may be unreal. A set of cumulative estimates are given for the number of pups born in each year since 1950. These cumulative estimates depend on the estimate of the ratio of survival of females to males from birth to age 3. An estimate of this ratio is given. The implications of this study on the population dynamics model of the fur seal are reviewed: in particular while the exact model is less definite, the suggested optimum population level is almost unchanged from that suggested in earlier studies.

Nagasaki (1961) and Chapman (1961) have published models of the population dynamics of the Pribilof fur seal which, while based on different hypotheses, lead to very similar conclusions. These have been summarized in a report of the North Pacific Fur Seal Commission (PFSC).[2] Both models are based upon estimates of the pup population from tag recoveries.

Such studies of population dynamics are basic to a proper management of the fur seal herds, both to maximize yield and to evaluate the effect of the herd on other living resources of the sea. Moreover the application of methods to this population which has been extensively studied and for which much data are available, are useful; such applications show up the strength and weakness of theoretical procedures and pave the way for a more intelligent application to other valuable marine resources for which studies are in much earlier stages.

Both authors also noted that there are two basic unresolved questions:

1. Why did the population estimates increase sharply from 1952 to 1956 and drop suddenly from 1956 to 1957?

2. Why do estimates of male survival to age 3 and the estimates of the female population derived from the tagging estimates lead to the conclusion that the survival rate of females from birth to age 3 is much greater than that of males?

The large fluctuations in the pup population as suggested by the estimates do not seem reasonable when the population of breeding females consists of 10 or more age classes. The survival advantage of human females is well known, and there is some evidence of this in other mammalian populations, but the differences are at most a few percent. In an earlier study, however, I suggested that the survival advantage of females over males is 2 to 1 or more.

This study was undertaken with the aim of attempting to determine (1) if the fluctuations in the pup population estimates could be real, and (2) if the differential survival ratio might be much smaller than 2 to 1 or if the differential existed at

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[2] North Pacific Fur Seal Commission, 1962. North Pacific Fur Seal Commission Report on Investigations from 1958 to 1961. Manuscript report, Washington, D.C. Frequent reference will be made to this report, hereafter called FSCR.

all. Actually it is convenient to treat the problems in the opposite order, looking first at all ways of estimating the female population. The apparent differential survival in favor of females could be explained in two ways: (1) Underestimation of the male survival, and (2) overestimation of the number of females based on the tag estimates and the pregnancy rate.

ESTIMATION OF MALE SURVIVAL

The survival of males to age 3 is estimated by adding to the number of returns as counted in the male kill, the estimated escapement of males from the kill. I need not comment on the first of these two factors, except to note that since the survival being calculated is natural survival the kill of a year class at ages other than age 3 has to be adjusted to this age. Thus, in natural conditions, the animals killed at age 2 would have been part of the 3-year-old returns, except for the mortality from age 2 to 3.

The estimation of the escapement (the number of males that survive to age 3 and are not then or later taken in the male kill) is a more complex problem. Such males form what is known as the breeding reserve; if they survive to sociological maturity (roughly age 7), they will become part of the bull herd.

ESTIMATION OF MALE ESCAPEMENT

The method of estimating male escapement was discussed in Kenyon, Scheffer, and Chapman (1954). The males survive the commercial kill either because they arrive at the islands after killing has ended near the end of July or because they are not of the proper sizes at the time of killing. Formerly, animals estimated by eye to be between 41 inches and 45¾ inches were those selected for the kill, and after being killed the animals were quickly measured from the tip of the nose to the base of the tail. This measurement served as a check on the selection but obviously did not prevent errors in selection. In some years the desired lengths have been modified slightly, and more recently measurements have been made of a random sample and according to accepted mammalian procedures, with the selection procedures adjusted accordingly.

In general, any male measuring 40 inches or less in one summer and growing to more than 45 inches by the following summer might well have been spared. If the male survived to age 6 or 7, it would join the herds of harem or idle bulls. The possibilities of this are seen in the analysis of the data on lengths taken from FSCR tables 82 and 83 on pages 167–172. During the spring and early summer both groups grow at about 3.5 cm. pe month. The apparent discrepancy between thi figure and the small difference in means of the 3's and 4's (8.71 cm.) is easily explained. The commercial kill selects the larger of the 3-year-olds s that the surviving 4's are the smaller members o the year class. Little is known of growth during the other months of the year; undoubtedly i proceeds at a much slower rate in the less favorabl months, but a 5-month growth of 17.5 cm. (almos 7 inches) could change a seal from an undersize animal to an oversized one.

Because of the crude methods used in the pas for selecting seals and measuring their lengths estimation of escapement of the males from th kill has been unsatisfactory. The estimation o escapement due to time of arrival has been base upon a fitting of a normal curve to the kill by "rounds" (a round is a 5-day period in which al hauling grounds of an island are visited). Th escapement is estimated from the "tail" of this curve. This estimation has been satisfactory i terms of predicting the kill of 4-year-old males from the escapement of 3-year-olds. Nevertheless several questions remain unanswered in terms o estimates of the final escapement (i.e., the recruitment to the breeding reserve). For example: is the time of return really normally distributed? Do late returners in one year tend to be lat returners in the following year? Are there som animals that do not return to the islands at all a ages 3 or 4, but only return when more fully mature at a later age?

To partially resolve this question, we turn to th

TABLE 1.—*Mean lengths of pelagically sampled fur seal in the eastern Pacific, 1958–62* [1]

Age of seals	March	April	May	June	July
Age 3:					
Mean length (cm.)	98.7	102.4	106.2	109.0	113.
Number of seals taken	16	49	74	43	26
Age 4:					
Mean length (cm.)	110.0	110.0	115.3	117.8	121.
Number of seals taken	6	20	26	13	11

[1] Data for 1962 from U.S. samples only. Regression lines fitted to this dat yield for 3's: $L=106.0+3.56T$ and for 4's: $L=114.7+3.44T$, where in both case T is measured in months from mid-May.

lata on adult males—the harem and idle bulls. These have been counted annually since 1905 xcept for the war year 1942. The possible errors n the counts of idle bulls noted in Kenyon et al. 1954) are emphasized. To begin with the pelagic amples obtained in recent years are analyzed or mortality rate estimation. The pertinent ata are shown in table 2.

Assuming a constant mortality rate $\hat{a}$, the best stimate of this rate is by the Chapman-Robson 1960) formula

$$\hat{a}=1-\frac{x}{1+x-\frac{1}{n}}$$

vhere n=total number of animals taken

$\bar{x}$=mean age with the ages coded beginning with zero. Here $\hat{a}=0.36$.

In June and July the breeding animals are on he islands and not as susceptible to pelagic capure; therefore some selection may be involved. 'or this reason captures in these months have een excluded in the last column of table 2. The stimate of the annual mortality rate based on ge composition data from recaptures in months ther than June and July is 0.36, identical with he estimate from the whole data. One further heck is available on this. In 1960 and 1961 xcess bulls were killed on Robben Island by the J.S.S.R. (table 11 of FSCR). Their age classication is shown in table 3.

Since a complete age breakdown is not available, Ieincke's estimation procedure is used. This ields:

for 1960 $\hat{a}=0.37$; for 1961 $\hat{a}=0.32$;

for the combined data $\hat{a}=0.34$.

These rates are for a different herd, but their alues suggest that the rate given above for the Pribilof herd is of the right order of magnitude. As will be shown later this is much higher than the corresponding female rate.

ABLE 2.—*Age distribution of male fur seals taken off Alaska, 1958, 1960, and 1962*

Age (in years)	Number taken (all months)	Number taken (excluding June and July)
	35	22
	25	23
	19	11
	12	7
	9	7
	4	2
	4	3
	2	2

These data are compiled from FSCR table 30 and from Fiscus, Baines, and ilke (1964).

TABLE 3.—*Age classification of males, age 7 and above, killed on Robben Island, 1960–61*

Year	Age (in years)					Total
	7	8	9	10	10+	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
1960	463	356	166	94	184	1, 263
1961	354	353	237	67	103	1, 114
Total	817	709	403	161	287	2, 377

There remains to be estimated the mortality rate of males from ages 3 to 7 and also the number of idle bulls uncounted because they are at sea. On attempt to estimate both of these was based on the historical data. The following equation can be presented:

$$(E_1+E_2)S=(HM+\Delta H)+k(IM+\Delta I)$$

where E_1=animals reserved for the breeding stock (a practice in 1923–32)

E_2=escapement due to size or time of arrival: these animals are also reserved for the breeding stock but no count is made of them.

K=male kill

S=survival rate of males from ages 3 to 7

H=number of harem bulls

M=mortality rate of bulls

ΔH=increase in number of harem bulls

I=number of idle bulls

ΔI=increase in number of idle bulls

k=fraction of idle bulls on land

It is reasonable to assume that E_2 is proportional to E_1+K; hence writing $E_2=f(E_1+K)$ the equation is rewritten

$$[E_1+f(E_1+K)]S=(HM+\Delta H)+k(IM+\Delta I)$$

This equation holds for any year with the appropriate lag (4 years) between the counts on the left-hand side of the equation and those on the right. While the large variations in annual data preclude my using the equation with such data, I hoped that by averaging over a 5- or 10-year period I might be able to estimate the three unknowns f, S, and k. This presupposes that the fraction escaping the kill remains constant over the several periods involved, that the fraction of idle bulls at sea remains constant, and the seal counters have had the same definition of an idle bull throughout the period of these data. The method seemed promising because of the large variations in E (nearly 10,000 in the 1920's but more recently zero); however, when tried for the periods 1923–27, 1928–37, 1934–38, or for 1923–32, 1933–40, 1946–55, the method gave negative values for k. Some of the assumptions made, appear to be invalid.

One other source of information is available—the pelagic catches off Alaska in 1958, 1960, and 1962 (data from same sources as table 2).

TABLE 4.—*Comparison of male and female pelagic captures off Alaska, 1958, 1960, and 1962*

Month	Number of males age 7 and over taken	Number of females age 4 and over taken	Proportion of males to females
June	15	677	0.022
July	13	504	.026
Total	28	1,181	.024

As will be shown later, the herd of females 4 years old or older has in these years averaged about 600,000. Assuming that 80 percent of the females are in the water at any time (based on observations of Bartholomew and Hoel, 1953), this suggests that not more than 12,000 males are in the water. This figure is consistent with the male total (25,000) if these animals spend half their time in the water. More reasonable is the suggestion that harem bulls spend about one quarter of these 2 months at sea, while idle bulls spend half their time on land and half at sea. This suggests that the idle bull count should be increased by about 50 percent to give the correct total. I believe this to be a maximum figure.

Data to estimate the mortality rate from ages 3 to 7 are even more tenuous. A mortality rate of 50 percent in the first year and 20 percent per year thereafter from ages 1 to 3 would be in accord with the observed returns. The mortality rate probably will be lower for these ages than for the mature animals competing for harems, so I use a figure of 0.20 (annual rate) here.

From 1950 to 1959 the bulls recruited through escapement from years of uniform killing averaged about 25,000 (with the idle bull count multiplied by 1.5). The annual mortality of this number at a 0.36 rate is 9,000. The growth of the herd averaged about 1,000 per year so that the recruitment must have been 10,000. To produce this recruitment at age 7 required (if mortality is 0.20 at ages 3 to 7) an escapement of $\frac{10,000}{(0.80)^4}$ or abou 25,000.

During 1946–55 the annual male kill averaged 64,350 (25,000 represents a 40-percent escapement). This absolute total and percentage are both much higher than the estimates obtained by methods used formerly. It is clear now from the above analysis that these methods underestimated escapement. Even without allowing for idle bulls at sea and using a mortality rate from ages 3 to 7 of 0.15 the needed escapement for this period was 16,000. This escapement estimate of 25,000 which will be used hereafter as the best figure for the 1946–55 period, applies to both islands. A corresponding estimate for St. Paul only is 80 percent of this, i.e., 20,000.

ESTIMATION OF THE NUMBER OF FEMALES

PREGNANCY RATES

Estimation of the number of females has been based upon the pregnancy rate and the estimated number of pups born. The pregnancy rate is well estimated from pelagic samples for each age class but to get an average for the whole adult female population, the size of each age class must be known. The age-specific pregnancy rates have been in good agreement from year to year (table 5 and Chapman, 1961, p. 365).

The broad picture for the Pribilof fur seals seems to be that few females give birth at age 4 about 50 percent at age 5, 80 percent at age 6 and 80–90 percent at ages 7 to 10 Thereafter the pregnancy rate declines slowly with age Before obtaining a best estimate of the pregnancy rate for the whole female herd it is necessary to estimate the age composition.

A serious problem in studying the fur seal has been obtaining representative samples of the whole herd or of major components of it. There is segregation by sex and age at sea and on land. On land the segregation is in part a result of the differential behavior of pregnant females, which tend to come ashore on rookeries, and nonpregnant females, which come ashore on hauling grounds and at the edges of rookeries. This behavior is not without exceptions, and the two kinds inter-

TABLE 5.—*Pregnancy rates of northern fur seals* [1]

Age	North American		Asian	
	1952 sample	1958–61 samples combined	1952 sample	1958–61 samples combined
4	0.01 (80)	0.04 (375)	0.37 (288)	0.48 (1133)
5	.43 (28)	.45 (403)	.80 (211)	.83 (837)
6	.82 (49)	.76 (445)	.89 (120)	.86 (571)
7	.72 (39)	.80 (545)	.85 (99)	.89 (340)
8	.77 (55)	.85 (609)	.91 (80)	.89 (199)
9	.89 (35)	.90 (555)	.88 (58)	.90 (123)
10	.74 (31)	.89 (513)	.88 (72)	.89 (72)
10+	.75 (187)	.82 (2641)	.84 (124)	.75 (340)

[1] Figures in parentheses represent number of females in the sample. The rates for 1952 are taken from table G, page 82, of Taylor, Fujinaga, and Wilke (1955). The 1958–61 data are given in FSCR table 20, page 94.

mix. In particular, some animals that have given birth are killed with other females on hauling grounds. The pelagic samples show immediately that the youngest age groups are underrepresented. Table 6 shows the combined female catches of the U.S. pelagic research expeditions of 1958–61 off the Pacific Coast of North America. In discussing age-specific pregnancy rates I need to mention mortality rates, since the age composition of the female class is partly reconstructed on the basis of estimated mortality rates. The method of estimating mortality rates (table 6) is given below.

Sampling below age 8 is unrepresentative, but if it is assumed that sampling is representative for age 8 and up, then mortality or survival rates can be estimated from these data. After study, I decided that the most satisfactory fit is obtained with a Gompertz curve, a form used for actuarial studies. The fitted curve is:

$$Y=6.9143-(0.5109)\ (1.1714)^{-X}$$

where Y represents ln (number) and X is age.

The rather low mortality rates during ages 3–10 are in close agreement with those used in Kenyon et al. (1954, p. 39), based on fewer data and estimated more crudely.

TABLE 6.—*Age composition of female seals taken by U.S. research vessels, 1958–61 combined, and estimated mortality rates*

Age	Females taken	Mortality rate [1]	Age	Females taken	Mortality rate
Years	*Number*	*Percent*	*Years*	*Number*	*Percent*
			14	336	0.226
			15	293	.265
		0.040	16	233	.311
	267	.046	17	142	.364
	307	.054	18	97	.426
	324	.064	19	59	.499
	407	.075	20	21	.585
	478	.088	21	16	.685
	447	.103	22	6	.803
	434	.120	23	3	.940
	429	.141	24	3	
	387	.165	25		
	362	.193	26	1	

[1] Percent of each age class dying during the year.

This composite sample (table 6) can also be compared with the 1952 pelagic sample (Taylor et al., 1955, p. 49). Since, in the 1952 sample, ages above 10 were not identified, it is possible only to use a Heincke-type estimate, i.e., the relation of the age 10 group to the 10-year and older animals. For 1952 the average mortality by this method for the 10+ group of females is estimated as 0.142, while from the composite sample (table 6) it is estimated as 0.154. The two estimates are in reasonable agreement.

The rates estimated here are somewhat lower than those given by Chapman (1961, p. 365), based upon the assumption of a constant mortality rate above age 9. More careful scrutiny of the data suggests that mortality increases with age. The average for the female population given in the 1961 paper was 0.14, here it is 0.11. The latter rate is used in the present study but, where pertinent, the implications of the higher rate will be considered.

What are the annual fluctuations in the pregnancy rate? Using the same age distribution and applying the age-specific pregnancy rates obtained in pelagic samples for 1952 (table 5) and for 1958–62 (Fiscus, Baines, and Wilke, 1964, p. 36) the following weighted averages are obtained: 1952, 0.595; 1958, 0.629; 1959, 0.629; 1960, 0.625; 1961, 0.588; and 1962, 0.578. The standard deviation of the six rates is 0.023, which is about 3.8 percent of the average.

A stable herd with these age-specific mortality rates and the age-specific pregnancy rates of the 1958–61 combined samples (table 5) would have an overall pregnancy rate of 0.62. With the somewhat higher mortality rates used by Chapman (1961, p. 366), the estimated pegnancy rate was 0.58. Both rates apply to the female population of ages 3 and older. It is clear that the estimate of 0.6 used for pregnancy rate in Chapman (1961) may be adopted as the most reasonable.

CUMULATIVE ESTIMATES OF THE NUMBER OF FEMALES

The estimates made of mortality and pregnancy rates could be used to estimate the total number of females in any year, if the female recruitments at age 3 for several years past were known. But all that is known is the male kill by ages for year classes since 1947 and by size groups only for earlier years, together with the escapement estimates derived earlier. From 1940 to 1949 the average male kill was 53,840 per year. The escapement during this period may be estimated at 40 percent of this or 21,536, hence a reasonable estimate of the male survival to age 3 for these years is about 75,000. An estimate of 75,000 may be slightly high for the year classes prior to 1937, but by 1956 such year classes constituted a negligible part of the population or either males or females.

The estimated male natural survival to age 3 (if no 2-year-olds were killed) for the year classes 1947–59 is shown in table 7. This has been calculated using the 40 percent escapement figure for year classes for which killing terminated by July 31. For year classes that experienced an August kill, I have assumed that one third of the August 3-year-male kill and all the August 4-year-male kill represents animals that would have formerly been part of the escapement. Hence, the 40 percent escapement estimate is applied to the balance of the kill from the year class. Raw data for table 7 are found in FSCR table 6.

To estimate the female recruitment I need to know λ (lambda), the ratio of female survival rate to age 3 to the corresponding male survival rate. Because λ is not known, several values are tried, viz, λ=1.0, 1.25, 1.5, 2.0.

The basic procedure is illustrated with the 1956 estimate of the female population and with λ=1.0.

The cumulative estimate of the 3-year and older female population in 1956 is:

1953 year class survival to age 3×1.000=62,000 (1.000)

+1952 year class survival to age 3×0.960= +93,000 (0.960)

+1951 year class survival to age 3×0.915= +83,000 (0.915)

+1950 year class survival to age 3×0.866= +84,000 (0.866)

+1949 year class survival to age 3×0.810= +62,000 (0.810)

+1948 year class survival to age 3×0.749= +70,000 (0.749)

+1947 year class survival to age 3×0.683= +83,000 (0.683)

+1946 and earlier survival to age 3×3.013= +75,000 (3.013)

Total=685,000

TABLE 7.—*Estimated natural survival of males to age*
St. Paul Island, 1947–59 year classes

Year class	Total	Year class	Total
1947	83, 000	1953	62, 0
1948	70, 000	1954	44, 0
1949	62, 000	1955	55, 0
1950	84, 000	1956	21, 0
1951	83, 000	1957	56, 0
1952	93, 000	1958	79, 0
		1959	60, 0

The mortality factors are obtained from those shown in table 6 by successive multiplication.

The foregoing procedure is applied to othe years, with other values of λ (table 8). Th earliest estimates in the table are biased upwar by an overestimate of the contribution of the pre 1940 year classes. There is also some upward bia of the earlier estimates from tagging. In 196 and subsequently, a more intensive search for tag lost animals was undertaken, and it was demon strated that there had been some oversight earlier (A tag-lost animal is a seal that had been tagged and had lost the tag before recapture; it is identi fied as an animal that had been tagged by the checkmark that is also placed on the flipper at the time of tagging.) The largest estimate from tagging, however, is of the 1956 year class; the 1960 kill from this class was searched carefully for tags and tag-lost animals.

The last column of table 8 shows 10 different esti mates of λ, which are valid only if the tagging esti mates are valid.

If the annual mortality rates used here are too low, i.e., if the true rates are similar to the rates

TABLE 8.—*Cumulative estimate of 3-year and older female*
population, St Paul Island, 1950–62

Year	Postulated differential survival rate of females to males to age 3 (λ)				Best estimate of number of females from tagging estimate of pups[1]	Estimate o λ from tagging estimate of pups
	1. 00	1. 25	1. 50	2. 00		
1950	683	854	1, 024	1, 368	No estimate	
1951	677	846	1, 016	1, 354	813, 000	1. 2
1952	664	830	996	1, 328	[2] 828, 000	1. 2
1953	674	842	1, 011	1, 348	1, 140, 000	1. 6
1954	682	852	1, 023	1, 364	1, 203, 000	1. 7
1955	699	874	1, 048	1, 398	1, 240, 000	1. 7
1956	685	861	1, 034	1, 378	1, 337, 000	1. 9
1957	635	798	961	1, 288	955, 000	1. 4
1958	583	738	892	1, 201	967, 000	1. 6
1959	514	648	782	1, 050	1, 040, 000	1. 9
1960	483	610	736	989	[3] 828, 000	1. 6
1961	499	625	750	1, 001	(4)	
1962	468	593	719	970	(4)	
Average						1. 6

[1] Number of pups as estimated from male tag recoveries in commercia kill divided by best estimate of average pregnancy rate viz 0.6.

[2] Dead pup count estimated from counts of two areas to be 45,000. Note tha a slightly different estimate was used in table 2 of Chapman (1961, p. 359)

[3] Estimate based on returns of 3-year males only.

[4] Estimate not yet available.

given in Chapman (1961), then the present cumulative estimates are too high. This would yield even higher estimates of λ. If the tagging estimates are correct then the differential survival advantage of females at ages 0 to 3 is indeed large. The tagging estimates possess, however, internal inconsistencies, and the possible explanations for these are now considered.

FLUCTUATIONS IN THE APPARENT NUMBER OF PUPS BORN

Another unresolved question is: How could the estimated number of pups born, about 500,000 in 1947–49 and 1952, increase to 584,000 in 1953 in 722,000 in 1954, 744,000 in 1955, and 802,000 in 1956; then drop to 573,000–580,000 in 1957 and 1958? What are the possible explanations of the fluctuation? If there is no bias in the estimates from tagging, there are three explanations: (1) Sampling variations, (2) variations in the pregnancy rate and, (3) variations in the number of adult females.

SAMPLING VARIATIONS

The magnitude of sampling variations is discussed elsewhere (Chapman 1963).[3] I showed that the standard deviation of the 1952 or 1956 estimates is less than 20,000, so sampling variation can reasonably explain less than 60,000 of the 300,000 difference. Moreover, there are also the 1953 and 1954 estimates to explain.

VARIATIONS IN THE PREGNANCY RATE

Turning to variations in the pregnancy rate, it is unfortunate that there was no pelagic sample in 1956 nor, in fact, in the years of highest estimates from tagging. However, the samples taken in six different seasons have shown very similar rates, with the variation from highest to lowest of the mean annual rates being only 8.4 percent of the 6-season mean. Furthermore, such variations are inadequate to explain the apparent change in number of pups born, a 60 percent increase from 1952 to 1956. In fact, if the observed 1952 pregnancy rate and the 1952 pup estimate (497,000) were both true, the number of females in 1952 would have been 835,000. If this many females had 802,000 pups in 1956, the pregnancy rate was 0.96, a rate that is inconsistent with any data available.

VARIATIONS IN THE NUMBER OF ADULT FEMALES

Finally, was there a substantial increase in the number of females between 1952 and 1956? The cumulative estimates suggest, with $\lambda \leq 2$ that the change was 50,000 or less, accounting for a possible increase of about 30,000 pups.

No single cause explains the 1952–56 change; perhaps there was a combination of causes. Consider the 1952 pup estimate +2 standard deviations, i.e., 537,000. With λ pregnancy rate $P=0.595$ this means 903,000 females. Suppose that from 1952 to 1956 there was an increase to 968,000 femoles. Assume that in 1956 P was 0.653 (P+2 standard deviations). This suggests a 1956 pup crop of 6 9,000. Allowing for the sampling error in the 1956 estimate (2 standard deviations is less than 40,000), the unaccounted discrepancy is still 133,000. That all three factors (nonrepresentative sampling, variation in pregnancy rate, and variation in number of adult females) should act in the same direction in any given year is improbable. Even so, there remains a large unexplained discrepancy in the estimated number of pups born.

BIAS IN ESTIMATES FROM TAGGING

Some of the estimates of pups born from tagging must be biased, and the most likely cause is excess mortality caused by the tag or tagging operation. In general, the years with the poorest survival had highest estimates. An upward biased estimate would result from an increased tendency for tagged pups to die during the fall and winter. The tagging need not bring immediate mortality, though a 1962 experiment indicated that this may occur. Roppel et al. (1963) showed that the mortality on land of tagged pups counted during September was 2.7 times that of untagged pups (33 dead tagged pups expected, 84 dead tagged pups observed), however, such mortality in general appeared to be less than 6 percent of the mortality that occurred prior to the tagging period so that even this differential mortality does not explain the excess mortality postulated to account for the excessive tagging estimates. Consequently, this is a hypothesis rather than a firm fact.

Tagging mortality may be greater in years when survival is poor, but this does not explain why survival has varied so greatly over the past several years. A population at or near its ceiling is expected to fluctuate more widely than one that is actively growing, and, moreover, the range of fluctuation will tend to increase with time through purely random causes. The largest fluctuations in the fur seal herd will be brought about by random fluctuations in survival of the youngest animals, though fluctuations in the pregnancy rate may also contribute some variability.

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[3] Douglas G. Chapman. 1963. Problems in the analysis of tagging experiments with particular reference to Alaska fur seal data. To be published.

A possible explanation also may be found in external factors. Abegglen, Roppel, Johnson, and Wilke (1961)[4] speculated about the relationship between the average temperature for the preceding year and the dead pup counts. They reported the correlation between these variables to be −0.853, which is significant at the 1 percent level. The correlation between average temperature and total male survival for the year classes 1950–59 is 0.924, which is also highly significant and even higher numerically than the correlation between dead pup counts and temperature. Data are not yet available for survival from subsequent year classes. The temperatures considered are for the St. Paul Island weather station. It would be more useful to have water temperature for the Bering Sea. Without such data it is only possible to speculate that water temperatures are rather closely related to land temperatures with, however, some lag. A lower water temperature might have a direct effect on the young seals or it might reduce their food supply. Either could result in increased mortality on land during the summer and at sea during the fall and winter. A model I proposed (1961) was based on food at sea as the limiting factor on growth of the pup. Clearly, temperature dependence would be more important if the population were pressing on its food supply than if it were not.

In summary, the tagging estimates show fluctuations that are not explicable in terms of the structure of the herd and known values of other parameters and which therefore suggest some bias is inherent in the estimates. It is, therefore, important to turn to other methods of estimating λ or the female herd size.

DICHOTOMY ESTIMATES

Another method of population estimation i based upon differential kill of the sexes (Chapman, 1955). This method appears to be idea for the fur seal where in excess of 70 percent o the males are killed at ages 3 or 4, but only small proportion of the females is removed. However, the method also requires estimates of the se ratio before and after the differential kill. Whil these are available from large pelagic samples i 1958–61, the segregation of the sexes at se creates difficulties. If the segregation pattern remains constant from year to year, these difficultie might be overcome. The following model wa considered:

Let N_1, N_2 be the number of males and females respectively, at the beginning of any summe season. Define $N=N_1+N_2$. Assume that a proportion ϕ_i of the N_i are to be found in any area a sea in any season. Then the proportion of male at sea in this area and season will be

$$p'=\frac{\phi_1 N_1}{\phi_1 N_1+\phi_2 N_2}=\frac{N_1}{N_1+\phi N_2} \qquad (1)$$

where

$$\phi=\frac{\phi_2}{\phi_1}$$

Let R_i be the kill of the N_i in the summer season and s_i the rate of natural survival during the following winter. Then the proportion of males at sea in the same area next spring will be

$$p''=\frac{N_1-R_1}{(N_1-R_1)+\phi s(N_2-R_2)} \qquad (2)$$

where

$$s=\frac{s_2}{s_1}$$

and where all that needs to be assumed is that ϕ, the ratio of ϕ_2 to ϕ_1, remains constant between years.

If N_1 refers to the number of males at age 3, this can be assumed known, and if information is available as to s, then observations of p', p'' from pelagic data can be used to estimate ϕ and N_2. In particular, it is reasonable to assume that s equals 1, approximately, since both s_1 and s_2 are close to 1.

Writing $N_2=\lambda N_1$ and setting $s=1$ equations (1) (2) may be rewritten

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[4] Carl E. Abegglen, Alton Y. Roppel, Ancel M. Johnson, and Ford Wilke. 1961. Fur seal investigations, Pribilof Islands, Alaska, Report of field activities, June–November 1961. Bureau of Commercial Fisheries, Marine Mammal Biological Laboratory, Seattle, Wash.

$$\frac{1}{p'}=1+\phi\lambda;\ \frac{1}{p''}=1+\phi\left(\frac{\lambda N_1-R_2}{N_1-R_1}\right)$$

or

$$\phi=\frac{1-p'}{\lambda p'}$$

Substituting this last equation in $\frac{1}{p''}$ yields

$$\frac{1-p''}{p''}=\frac{1}{\lambda}\left(\frac{1-p'}{p'}\right)\frac{\lambda N_1-R_2/\lambda}{N_1-R}$$

Put

$$\frac{(1-p'')p'}{p''(1-p')}=Q$$

Then

$$Q=\frac{N_1-R_2/\lambda}{N_1-R}$$

or

$$(N_1-R)Q-N_1=-R_2/\lambda$$

Changing signs and taking reciprocals produces an equation for λ:

$$\lambda=\frac{R_2}{N_1-Q(N_1-R_1)} \tag{3}$$

The following estimates of λ were obtained from the indicated pelagic samples (from which estimates of p', p'' were obtained). The year in the second column refers to the first year of the paired samples and the year for which the N_1 estimate is determined.

The tagging results and other data suggest that λ should be 1 or greater. The estimates of λ from table 9 are quite unreasonable. This may be due to failure of the basic assumption that the proportion of males to females in any one area and season remains constant from year to year. The estimates of λ by the dichotomy method depend primarily on the size of R_2. In the standard application of the dichotomy method, the greater the difference between R_1 and R_2, the better the estimation of population size; however, with these data this is not so. Perhaps the R_2 values are too small. Also, the small size of the pelagic samples—when only one age-sex class is considered—makes correspondingly great variability in p', p''. I attempted to combine data from different years to eliminate or reduce the variability, but the results proved equally unsatisfactory and are not shown here.

POPULATION DYNAMICS OF THE FUR SEAL HERD AND ESTIMATION OF THE NUMBER OF FEMALES

Recent data do not permit resolving the question: What is the value of λ, the ratio of female to male survival from birth to age 3? There are also the data of the early 1920's when counts were made of the number of pups born. Both sets of data are considered below.

We have the obvious fundamental relationship (equation 4):

$$\frac{PS}{2}=(a+g)(1+g)^2 \tag{4}$$

where

P=proportion of females age 3 and older that are pregnant in any one year

S=survival rate of pups (female) from birth to age 3

a=annual mortality rate (average) of female population

g=annual growth rate of female population

The factor one-half on the left-hand side arises from the assumption that half of the pups born are females, which is consistent with all available information. The factor $(1+g)^2$ on the right-hand side follows because of the time lapse from

TABLE 9.—*Estimate of λ, ratio of differential survival of females to males, by dichotomy method*

Area	Year	Age group	p'	p''	R_1	R_2	N_1	λ
Washington	1958	3	0.0	0.06	35,109	11,393	68,000	0.17
Do	1959	3	.33	.25	12,922	2,016	25,000	.29
Do	1960	3	.27	.15	29,381	281	66,000	−.02
Do	1960	4	.25	.07	4,149	562	10,000	−.04
British Columbia	1959	3	.33	.10	12,922	2,016	25,000	−.05
Do	1960	3	.38	.20	29,381	281	66,000	−.01
Do	1961	3	.40	.17	57,871	4,534	96,000	−.14
Do	1961	4	.20	.08	19,836	6,776	31,000	−15.5
California	1958	3	.03	.06	35,109	11,393	68,000	.23
Alaska	1958 (June)	3	.80	.33	35,109	11,393	68,000	−.06
Do[1]	1958 (before June)	3	.85	.28	48,489	18,560	68,000	−.09

[1] 1958 and 1960 pelagic samples are combined so that R_1, R_2 represent the combined kill of 3s in 1958 and 4s in 1959 for this calculation.

birth to recruitment. It can best be shown by the following diagram:

Year	0	1	2	3
Number of females	N	$N(1+g)$	$N(1+g)^2$	$N(1+g)^3$
Increase	----------	----------	$N(1+g)^2g$	----------
Mortality	----------	----------	$N(1+g)^2a$	----------
Number of female pups	$\frac{NP}{2}$	----------	----------	----------
Survivors	----------	----------	$\frac{NPS}{2}$	----------

The recruitment (survivors) must account for growth and mortality losses, whence we have equation (4) above. This equation, of course, is trivial. What is significant is how P, S, and a change as the population changes from a growing one to a stable one.

For later purposes it is convenient to rewrite (4) as (equation 5):

$$\frac{PS'\lambda}{2}=(a+g)(1+g)^2 \qquad (5)$$

where S'=survival rate of male pups from birth to age 3 and as before

λ=differential survival of females to males (from birth to age 3)

From data of the early 1920's (Chapman, 1961) the St. Paul kill from the 1920–22 year classes averaged 13,590 (size groups 2, 3, 4). In addition, 22,666 were reserved for the breeding stock in these 3 years (average, 7,555 per year). Adding these two and also adding an estimated 40 percent escapement yields an average male survival of 30,000. Since the average pup count was 150,000 (half male and half female) the estimate of S' is 0.40.

Early pup counts (Kenyon et al., 1954, p. 20) show that the 1916–22 annual rate of increase was 0.08 on St. Paul Island. The St. George rate of increase, however, was 0.07, and the 1920–24 St. Paul annual rate of increase was 0.07. The latter is based on partial counts, but it is likely that the growth rate would begin to decrease about this time, so g is taken to be 0.07. At present the growth of the Asian herds as measured by the pup counts is 8–9 percent annually.

Unfortunately, the values of P and a are not known for 1916–22. It is possible, however, to calculate λ for a range of reasonable values of P and a, assuming that P was no smaller than at present and a no larger. Values for λ are shown in table 10.

Table 10.—*Values of* λ *(differential survival of females to males) corresponding to various possible values of* P, *pregnancy rate, and* a, *annual mortality rate (1920's data)*

Values of P	Values of a				
	0.11	0.10	0.09	0.08	0.07
0.6	1.72	1.62	1.53	1.43	1.34
0.7	1.47	1.39	1.31	1.22	1.14
0.8	1.29	1.22	1.14	1.07	1.00

Such a table does not provide a close estimate of λ but it does suggest that it was then larger than 1. Concerning the value of P (the pregnancy rate) and a (the annual mortality rate), the following comments are pertinent. If the observed age-specific pregnancy rates from western Pacific samples (1958–61) shown in table 5 are applied to the eastern Pacific age distribution, the resulting pregnancy rate for the whole population would be 0.70. The pregnancy rate of the females on the Asian islands must be slightly higher than this since there is some intermixture of Pribilof seals in these western Pacific samples. To allow for this, average intermixture rates have been calculated from table 43 of FSCR (p. 120). For ages 3 to 6 these averages are 0.18, 0.22, 0.42, and 0.70 (when the dashes are correctly interpreted as zeros). This yields adjusted intermixture rates for those ages of 0.12, 0.60, 1, and 1, respectively.

The equation to determine these adjusted rates is:

$$\pi_pP_p+\pi_AP_A=P_w$$

or

$$P_A=\frac{P_w-\pi_pP_p}{\pi_A}$$

where

π_p=proportion of Pribilof seals in western Pacific samples

π_A=proportion of Asian seals in western Pacific samples

P_p=pregnancy rate of Pribilof seals

P_A=pregnancy rate of Asian seals

P_w=observed pregnancy rate of western Pacific samples

For 4-year-olds the equation becomes

$$(0.04)+(0.78)P_A=0.48 \text{ or } P_A=0.60 \qquad (22)$$

Since the estimates for ages 5 and 6 are impossible, we have used the maximum observed rate, or 0.90, for these ages and for ages 7 and 8 where no intermingling estimates are available. The resulting adjusted pregnancy rates (Asian females) are as follows: Age 3, 0.13; age 4, 0.60; ages 5–9, 0.90; age 10, 0.89; age 10+, 0.75; weighted mean, 0.74.

It seems, therefore, that 0.80 is a reasonable upper limit for the pregnancy rate of the early Pribilof herd.

There is little direct information available as to the annual mortality rate in the early 1920's. The present age distribution of the western Pacific samples suggests higher mortality rates than for the eastern Pacific samples. I do not know whether this is due to nonrepresentative sampling or to a variable intermixture of Pribilof seals. With a growing population the proportion of younger animals would be greater. According to the model given earlier (pages 21 and 22) younger seals have lower mortality rates, so that the average rate for the whole herd would be reduced. The reduction due to this cause would be slight.

Turning to the present data we have $a=0.11$, $g=0$, $P=0.6$ so that equation (5) yields:

$$s'\lambda=0.37$$

Since it is reasonable to suppose s' is less now than in a growing herd $s'\leq 0.40$, whence $\lambda\geq 0.925$. If the 1947–49 and 1952 tagging estimates are accepted (Chapman, 1961, tables 2 and 3) $s'=0.294$ so that $\lambda=1.27$. These agree very closely with the estimates of λ from 1951 and 1952 in table 3. The latter were based on a comparison of cumulative and tagging estimates of the female population. Too much importance must not be attached to this agreement, since essentially the same supporting data are involved.

BEST ESTIMATE OF λ

At the present time there seems to be no best estimate of λ. The data indicate a range of values and suggest that λ is probably slightly greater than 1. A reasonable value for λ from the 1920's data is approximately 1.25, which is also consistent with the 1947–49 and 1952 tagging data. This value is adopted here as best. Higher values of λ are possibly consistent with the available data but seem biologically less reasonable.

IMPLICATIONS FOR THE POPULATION DYNAMICS OF THE FUR SEAL HERD

The population models of both Nagasaki (1961) and Chapman (1961), utilized the high estimates from tag recoveries of the 1952–56 period. If such estimates are discounted, then the right-hand limb of the parent-progeny relationship (e.g., Chapman, 1961, fig. 1, p. 361) and hence the probable optimum population level is much less well defined.

Nevertheless, the models fitted in my earlier paper may still be fitted either to data from tagging estimates through 1952 or to the cumulative estimates. The results in either case are similar and differ very little from the equations given in the earlier paper. For example, using the cumulative estimates (with $\lambda=1.25$) for the period 1950–59 the average female population was 814,300 which with a pregnancy rate of 0.6 produced an annual pup crop of 489,000. The male survival to age 3 from three-year classes averaged 64,000. Combining this with the 1920's data yields:

$$N_m=0.0293\ E^{3/2}-0.00106\ E^2 \text{ (Chapman model)}$$

or

$$N_m=0.2306\ E-0.000204\ E^2 \text{ (parabolic model)}$$

where

N_m=male survival to age 3 (in thousands)

E=number of pups born (both sexes, in thousands)

From these equations the maximum sustainable yield (with $\lambda=1.25$, $P=0.6$, and an average mortality rate of the females 3 and older equal to 0.11) is attained when

$$E^{x}=351 \text{ (Chapman model)}$$

or

$$E^{xx}=366 \text{ (parabolic model)}$$

The estimated male return at these levels would be 64,000 or 57,000 according to the two different models. Of these, about 71 percent or perhaps somewhat more would be available for the commercial harvest. The sustainable female yield according to these equations is 14,000 (Chapman model) or 7,000 (parabolic model).

If the female mortality rates are underestimated, the $E^x E^{xx}$ values given here are slightly high and so are the levels of sustainable kill. On the other hand if the pregnancy rate should increase as the female herd is reduced, the effect would be an opposite one. Such an increase in P may occur only with some time lag.

If we accept the hypothesis that the estimates from tagging since 1953 have been inflated, possibly by tagging-induced mortality, immediate or delayed, and that the best estimate of λ, the ratio of female to male survival from birth to age 3 is about 1.25, then the best estimate of the average 3-year and older female population for 1960–62 is about 609,000. If P, the pregnancy rate, is about 0.6 this implies the average number of pups born in these years was 365,000, very close to the current best estimate of the optimum.

In conclusion, the figures on population sizes, harvests, etc. apply to St. Paul Island. The figures for the Pribilof herd as a whole can be obtained by the usual extrapolation.

In recent years a method of fall sampling has been developed to estimate the number of pups in the year of birth. While this procedure also has biases that are not yet fully resolved, preliminary results indicate strongly that the actual year classes are much less than have been indicated by tagging estimates. Some of the preliminary results are shown in Roppel et al. (1964); additional results of the improved 1963 experiment are to be found in the unpublished annual report of fur seal investigations for 1963.[5]

SUMMARY

1. This study was undertaken to review critically the unresolved questions about Pribilof fur seal population estimates—the apparent large fluctuations in the number of pups born and the apparent differential survival of males and females from birth to age 3.

2. The adult male annual mortality rate is estimated from pelagic samples to be 0.36; the age distribution of the much larger samples from the adult females taken pelagically are fitted by a Gompertz-Makeham curve. The average annual mortality rate for these adult females is estimated to be 0.11.

3. From counts made in the 1920's, and tagging estimates of 1947–49 and 1952, the best estimate of the ratio of female to male survival from birth to age 3 appears to be about 1.25.

4. This estimate of the differential survival ratio of 1.25 is used in computing a cumulative estimate of the female population 3 years old and older. The best cumulative estimate of the St. Paul Island adult female population is 854 thousand in 1950 fluctuating slightly to 861 thousand in 1956 and decreasing thereafter to 593 thousand in 1962.

5. Possible explanations for the fluctuations in the tagging estimates for post-1952 year classes are reviewed, and it is shown that these are inadequate to explain the magnitude of the changes. The tagging estimates have been biased by tag mortality, and such tag mortality is heaviest in year classes that have poor overall survival. Variations in overall survival may be due to temperature changes that are important at a high population level.

6. An unsuccessful attempt is made to estimate the female herd by a dichotomy method to resolve the contradiction between cumulative and tagging estimates.

7. Equations relating male survival to the original pup population on St. Paul Island are recalculated using the new data and from these the optimum pup population levels determined. These are estimated to be 351–366 thousand pups which corresponds at present pregnancy rates to approximately six hundred thousand adult females.

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APPENDIX

COMPARISON OF U.S.S.R. COUNTS AND TAGGING ESTIMATES

Because it has been possible to count the pups on the Asian islands we hoped that these counts would shed light on the validity of the tagging estimates there, and by implication, on the Pribilof estimates. Unfortunately, the comparison of counts and estimates on the different areas are contradictory. On Robben Island, where the counting is easy and is believed to be reliable, the counts and estimates (allowing for tag loss of the same order of magnitude as occurs with Pribilof tags) agree (appendix table 1). On the Commander Islands, where counting is difficult and less reliable, the estimates from tagging and the actual counts disagree markedly (appendix table 2).

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[5] Alton Y. Roppel, Ancel M. Johnson, Douglas G. Chapman. 1964. Fur seal investigations, Pribilof Islands, Alaska, 1963. Marine Mammal Biological Laboratory, Seattle, Wash.

The estimates from tagging are high because of tag loss, and to a very slight degree because some seals in the kill came from other islands. If the latter factor is ignored, the Robben Island data of appendix table 1 can be used to estimate the tag-lost/tagged ratio. To make N agree with the counted total, s should have been 1,236 for the 1958 year class and 938 for the 1959.

Appendix Table 1.—*Robben Island estimates from tagging*[1]

Year class	Year of recovery	Males killed (n)	Pups tagged (t)	Tagged males in kill (s)	$N=\frac{(n+1)(t+1)}{s+1}$	Pups counted
		Number	*Number*	*Number*	*Number*	*Number*
1958	1961–62	4,932	7,225	911	38,077	28,813
1959	1962	3,080	9,015	587	47,242	29,598

[1] Data from FSCR.

Appendix Table 2.—*Commander Islands estimates from tagging*[1]

Year class	Year of recovery	Males killed (n)	Pups tagged (t)	Tagged males in kill (s)	Adjusted[2]	$N=\frac{(n+1)(t+1)}{s^1+1}$	Pups[3] counted
		Number	*Number*	*Number*	*Number*	*Number*	*Number*
1958	1961–62	4,593	4,887	277	377	59,406	38,100
1959	1962	3,570	7,971	248	397	71,528	41,200

[1] Data from FSCR.

[2] $s^1=1.36\,s$ for 1958 year class and $s^1=1.60\,s$ for 1959 year class.

[3] The 1958 count was marked as incomplete. In FSCR an attempt was made to correct for this. Revised figures are here taken from Report on U.S.S.R. Fur Seal Investigations in 1963, V. A. Arseniev, 1963, p. 34. These are based on counts in subsequent years.

Hence we have

Tag-lost/tagged ratio

$$=\frac{1236-911}{911}=0.36 \text{ (1958 year class)}$$

$$=\frac{938-587}{587}=0.60 \text{ (1959 year class)}$$

The estimate for the 1958 year class is very similar to the tag-lost estimates for the Pribilofs; the larger 1959 value is not higher than the highest observed on the Pribilofs.

These tag-lost estimates have been applied to the Commander Islands recovery data (appendix table 7).

Even allowing for tag loss, the estimates greatly exceed the counts. The estimates may be about 10 percent too high because of the presence of Pribilof animals in the kill. The bulk of the discrepancy is unexplained; whether due to tag mortality or some other cause is unknown. The discrepancy can be used to support the contention that the Pribilof tagging estimates are also in error.

LITERATURE CITED

Bartholomew, George A. Jr., and Paul G. Hoel.
1953. Reproductive behavior of the Alaska fur seal, *Callorhinus ursinus*. Journal of Mammalogy, vol. 34, No. 4, pp. 417–436.

Chapman, Douglas G.
1955. Population estimation based on change of composition caused by a selective removal. Biometrika, vol. 42, parts 3 and 4, pp. 279–290.
1961. Population dynamics of the Alaska fur seal herd. Transactions of the 26th North American Wildlife and Natural Resources Conference, pp. 356–369.

Chapman, D. G., and D. S. Robson.
1960. The analysis of a catch curve. Biometrics, vol. 16, No. 3, pp. 354–368.

Fiscus, Clifford H., Gary A. Baines, and Ford Wilke.
1964. Pelagic fur seal investigations, Alaska waters, 1962. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 475, 59 pp.

Kenyon, Karl W., Victor B. Scheffer, and Douglas G. Chapman.
1954. A population study of the Alaska fur seal herd. U.S. Fish and Wildlife Service, Special Scientific Report—wildlife No. 12, 77 pp.

Nagasaki, Fukuzo.
1961. Population study on the fur seal herd. Tokai Regional Fisheries Research Laboratory, Special Publication No. 7, 60 pp.

Roppel, Alton Y., Ancel M. Johnson, Richard D. Bauer, Douglas G. Chapman, and Ford Wilke.
1963. Fur seal investigations, Pribilof Islands, Alaska, 1962. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 454, 101 pp.

Taylor, F. H. C., M. Fujinaga, and Ford Wilke.
1955. Distribution and food habits of the fur seals of the North Pacific Ocean. Report of Cooperative Investigations by Governments of Canada, Japan, and United States of America, February–July 1952. Washington, D.C., Government Printing Office, 86 pp.

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